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Evolution of Branchiostegals and Classification of Teleostome Fishes

by D. E. McAllister

Canada 1968

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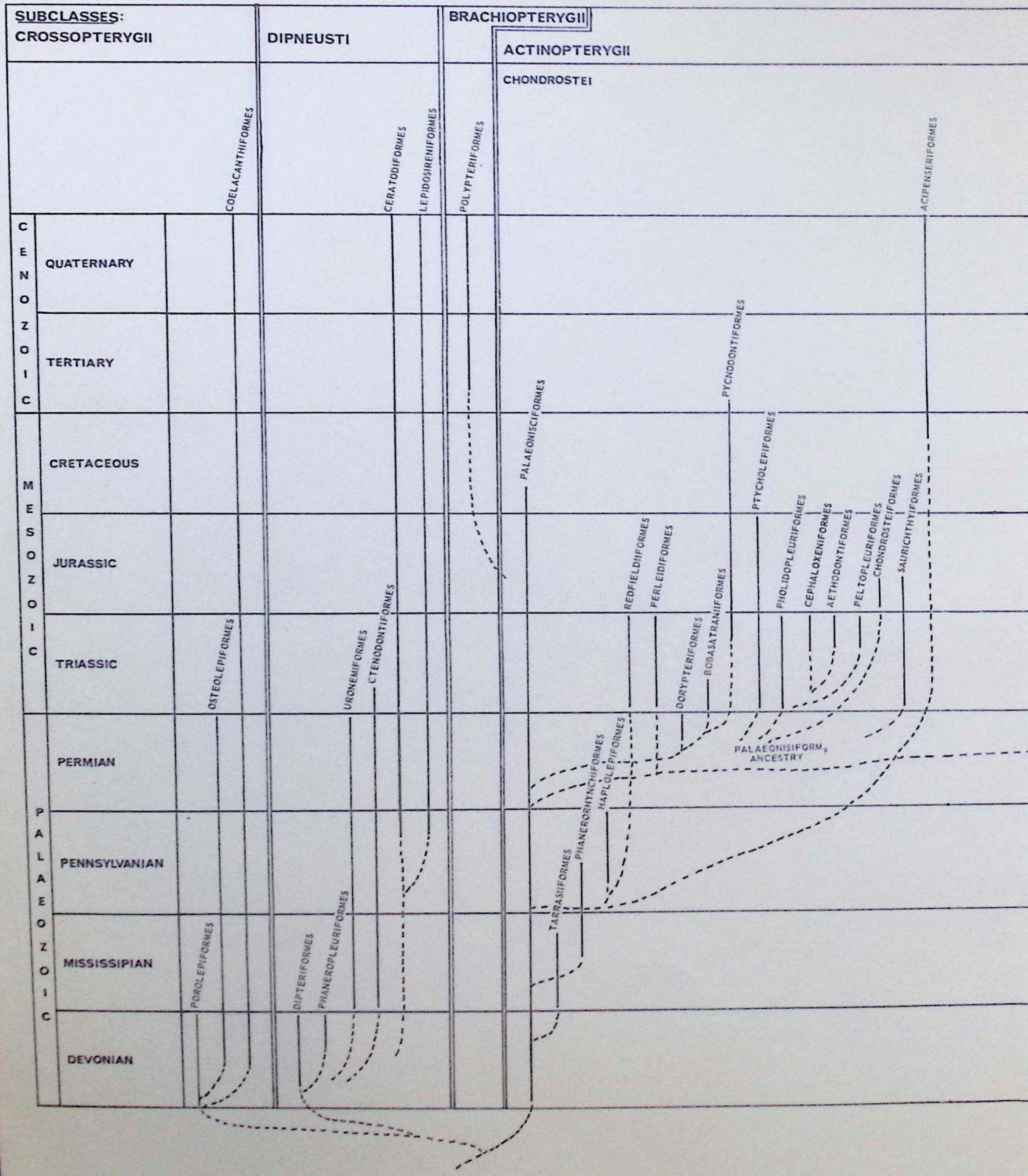
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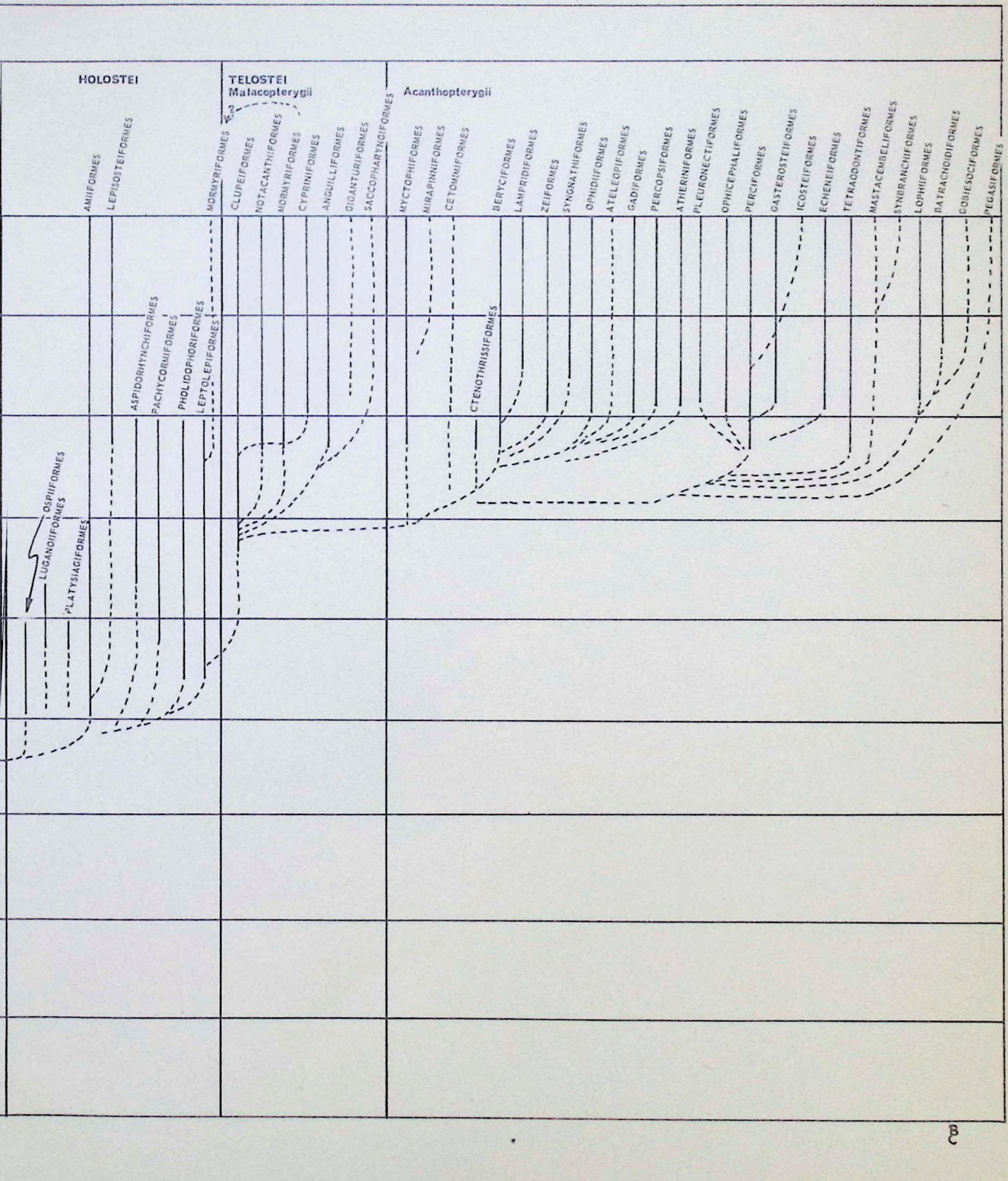
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LOPHIIFORMES
BATRACHOIDIFORMES
GOBIESOCIFORMES
PEGASIFORMES

B

EVOLUTION OF BRANCHIOSTEGALS AND THE CLASSIFICATION OF TELEOSTOME FISHES

CANADA

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Secretary of State

THE EVOLUTION OF BRANCHIOSTEGALS

AND ASSOCIATED OPERCULAR, GULAR, AND HYOID BONES

AND THE CLASSIFICATION OF TELEOSTOME FISHES, LIVING AND FOSSIL

by D. E. McAllister

Ottawa, 1968

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Acknowledgments

The basis of this study was a doctoral thesis at the Institute of Fisheries, University of British Columbia (McAllister, 1964). For aspects of embryology, function, and adaptive evolution that are not included here the reader is referred to the thesis.

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Résumé

1. Les branchiostèges, les operculaires, les gulaires et les parties inférieures de l'arc hyoïde d'un spécimen au moins de quelques 245 familles de téléostomes furent examinés. On a employé l'alizarine, et des specimens skelettiques et alcooliques. On a aussi puisé, dans la documentation, des données sur ces familles et sur les autres. Des formes de fossiles furent aussi comprises dans l'étude mais les données y relatives ont été entièrement puisées dans la documentation.
2. Le nombre et la forme des éléments des séries de branchiostèges (operculaires, branchiostèges et gulaires) et de l'arc hyoïde (interhyal, épihyal, cératohyal et hypohyal) ont été examinés, définis, décrits et représentés.
3. Les implications phylogénétiques de ces caractères complexes ont été vérifiées à l'aide d'un certain nombre d'autres caractères taxonomiques sérieux. Là où les changements suggérés par les deux complexes étaient appuyés par d'autres caractères, des changements furent apportés à la classification des téléostomes. Dans les autres cas, la classification existante ou les classifications précédentes furent renforcées, ou bien les complexes étaient différents de la plupart des autres caractères. Cette étude comprend les changement récents dans le classement et peut fournir un résumé utile de connaissance courante des poissons vivants et fossiles.
4. Les séries de branchiostèges et l'arc hyoïde présentent des caractères multiples d'importance systématique. Les formes ayant un grand nombre de branchiostèges se sont généralement révélées d'un groupe primitif (les exceptions sont indiquées). Les formes ayant des membranes branchiales séparées sont considérées plus primitives que celles avec des membranes branchiales unies et libres d'isthme ou celles avec des membranes branchiales jointes à l'isthme. Les téléostomes primitifs ont un seul hypohyal, les plus avancés en ont deux (mais parmi ces derniers, il y en a qui en perdent un ou les deux). La présence de gulaires médianes et latérales ou de plis gulaires est primitive. L'interoperculaire et apparemment l'épihyal sont absents chez les téléostomes primitifs.
5. Les deux complexes caractériels autorisent la division des Téléostomes en quatre sous-classes: les Actinopterygii, les Crossopterygii, les Dipneusti et les Brachiopterygii (quoique la dernière sous-classe n'est pas aussi distincte que les autres). Mais ils témoignent aussi d'une origine commune et d'une classification dans une seule classe (voir page 11).
6. Les deux complexes caractériels et autres traits ostéologiques autorisent le maintien des trois groupes importants des superordres: les Chondrostei, les Holostei, et les Teleostei, quoique avec une certaine modification des ordres inclus, et avec une certaine modification de

leur définition (voir pages 18–20). Les groupes ainsi reconstitués et redéfinis sont jugés naturels (sauf que certains groupes sont très peu connus pour la classification). Les Teleostei sont à leur tour divisés en deux groupes: les Malacoptérygii (voir page 33) et les Acanthoptérygii (voir page 89). La constitution et la caractérisation des deux derniers groupes ont été considérablement modifiées (voir table 2).

7. Voici quelques-uns des changements proposés. On trouvera d'autres changements moins importants aux passages pertinents du texte.
   - *a*) Les Mormyriformes offrent plusieurs ressemblances fondamentales avec les Osteoglossoidei (y compris les Pantodontidae) et les Notopteroidei (à l'exclusion des Hiodontidae). La conclusion est que les deux derniers groupes peuvent être rattachés à l'ordre des Mormyriformes (voir page 62).
   - *b*) Les Mormyriformes ont de commun avec les Leptolépiformes les os parasphénoïdes et hypohyause similaires, et ils se distinguent par ces mêmes traits, des Clupéiformes. Nous estimons que les Mormyriformes ont évolué à partir des Leptolépiformes ou leurs proches ancêtres et qu'ils doivent être classés parmi les Holostéens (voir page 63).
   - *c*) Les Elopoidei, les Albuloidei, et les Clupeoidei se distinguent du point de vue morphologique, et nécessitent une séparation de sous-ordre les uns des autres (voir page 35). Il peut y avoir plus qu'une espèce d'*Albula* (voir page 37).
   - *d*) Les Tselfatoidei appartiennent aux Clupéiformes primitifs, plutôt qu'aux Exocoetoides (voir page 43).
   - *e*) Les Hiodontidae ne sont pas étroitement liés aux Notopteridae et doivent être classés dans un nouveau sous-ordre des Hiodontoidei parmi les Clupéiformes (voir page 44).
   - *f*) Les Chanoidei (Kneriidae, Chanidae, Phractolaemidae, et Cromeriidae) se caractérisent par l'absence d'un interhyal ossifié et se distinguent par conséquent des Gonorhynchoidei qui possèdent un interhyal assez développé. D'autres caractéristiques permettent de croire en cette séparation (voir page 45).
   - *g*) Les branchiostèges et plusieurs autres caractères, autres que le squelette caudal, indiquent que les Esocidae sont plus primitifs que les Umbridae et les Dalliidae (voir page 57).
   - *h*) Le Crétacé, genre *Enchelurus*, précédemment compris parmi les Halosauridae, peut appartenir aux Anguilliformes primitifs (voir page 80).
   - *i*) Les Myctophidae et les Neoscopelidae se distinguent de tous les autres Myctophiformes par la possession de deux branchiostèges épihyause seulement, d'une vessie gazeuse et des photophores (voir page 90).
   - *j*) Un certain nombre d'ordres précédemment classés parmi les Malacoptérygii, sont classés parmi les Acanthoptérygii: les Myctophiformes, les Cetomimiformes, les Mirapinniformes et les Ateleopiformes (voir pages 89, 90, 99, 108).
   - *k*) Le *foramen des Béryciformes*: une grande perforation ovale au centre du cératohyal est caractéristique de plusieurs ordres primitifs Acanthoptérigiens (voir page 6).

     La *projection des Percopsidae*: on trouve la forme anguleuse de la base antérieure du quatrième branchiostège chez les

Ophidiiformes, les Gadiformes et les Percopsiformes (voir page 6).

La *saillie des Clupéoidei*: on trouve un gonflement élargissant la base antérieure des branchiostèges dans les clupéoides et certains de leurs dérivés (voir page 6).

l) Les Ophidioides doivent être séparés des Perciformes et associés avec les Gadiformes et les Ateleopiformes, en un nouvel ordre, les Ophidiiformes (voir page 114).

m) Les Amblyopsidae sont rattachée aux Percopsiformes (voir page 123).

n) Les Anabantoidei (y compris les Luciocephaloidei) et les Ophicephaloidei sont des Acanthoptérygiens étroitement reliés et se distinguent nettement des Perciformes, qui doivent être rattachés un même ordre des Ophicéphaliformes (voir page 133).

o) Les ordres des Bathyclupéiformes, des Polynemiformes, des Mugiliformes (en partie), des Coryphaeniformes, des Thunniformes et des Dactyloptériformes sont considérés des synonymes de l'ordre des Perciformes.

8. Les rapports généraux entre les ordres peuvent être constatés dans les figures 2 et 3. Le Tableau 1 présente un résumé des caractéristiques des structures étudiées dans les ordres variés. Les Tableau 2 expose sommairement les classifications de Regan, de Berg, de Bertin et d'Arambourg et de la présente étude (qui comprend les changements proposés par les auteurs récents). Les planches qui se trouvent à la fin du texte montrent les variantes dans les structures examinées.

Introduction[1]

This paper is a study of the variation and evolution of the branchiostegals and related elements in bony fishes. It considers two character complexes: the branchiostegal series (branchiostegals and, to a lesser extent, the related operculars and gulars) and the middle hyoid arch elements (interhyal, epihyal, ceratohyal, and hypohyals) upon which they may insert. These structures were studied to discover what reflections they might have on the ordinal phylogeny of the teleostomes. Indicated changes supported by other characters are united with the latest findings of other authors.

The study of single character complexes has advantages over the studying of many characters simultaneously. Parallelisms are more readily noted. Small but significant differences are less likely to be ignored. Some valuable single character complex studies may be noted: Hubbs (1920) on the branchiostegals; Starks (1930) on the bones of the shoulder girdle and (1926) on the ethmoid bones; Cockerell (1913) on the scales; Burne (1909) and Derscheid (1924) on the olfactory organ; Whitehouse (1910) and Gosline (1960, 1961) on the caudal skeleton; Gardiner (1963) on the snout bones; Emelianov (1935) on the ribs; Frost (1925, 1926, 1927, etc.) on the otoliths; Stensio (1947) on the sensory canals of the head; Lindsey (1956) on the vertical fins; Holstvoogd (1960) on the retractores arcuum branchialium; and Freihofer (1963) on the ramus lateralis accessorius.

None of these studies has included all the orders, and only one study has considered more than a hundred families.

In constructing sound phylogenies it is essential to employ as many good characters as possible. Therefore, in integrating the results of this study with existing classifications and in arranging the orders, numerous other structural features from the literature or from personal examination have been considered. These other characters include the following: the number of holobranchs; the composition of the upper jaw (premaxillaries, maxillaries, number of supramaxillaries); the presence of orbitosphenoid, clavicle, fulcra, subocular shelf, and fin spines; the nature of the scales; the number of vertebrae and pelvic rays; the position of the pelvics; the condition of the gas bladder; the types of ribs present; the caudal skeleton. Other characters including some from the studies noted in the previous paragraph were considered with particular groups.

LITERATURE

Branchiostegal counts have been used in fish taxonomy even before the time of Linnaeus. The more careful ichthyologists, such as Day, Regan, Smitt,

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[1] Manuscript submitted for publication 1 June 1965.

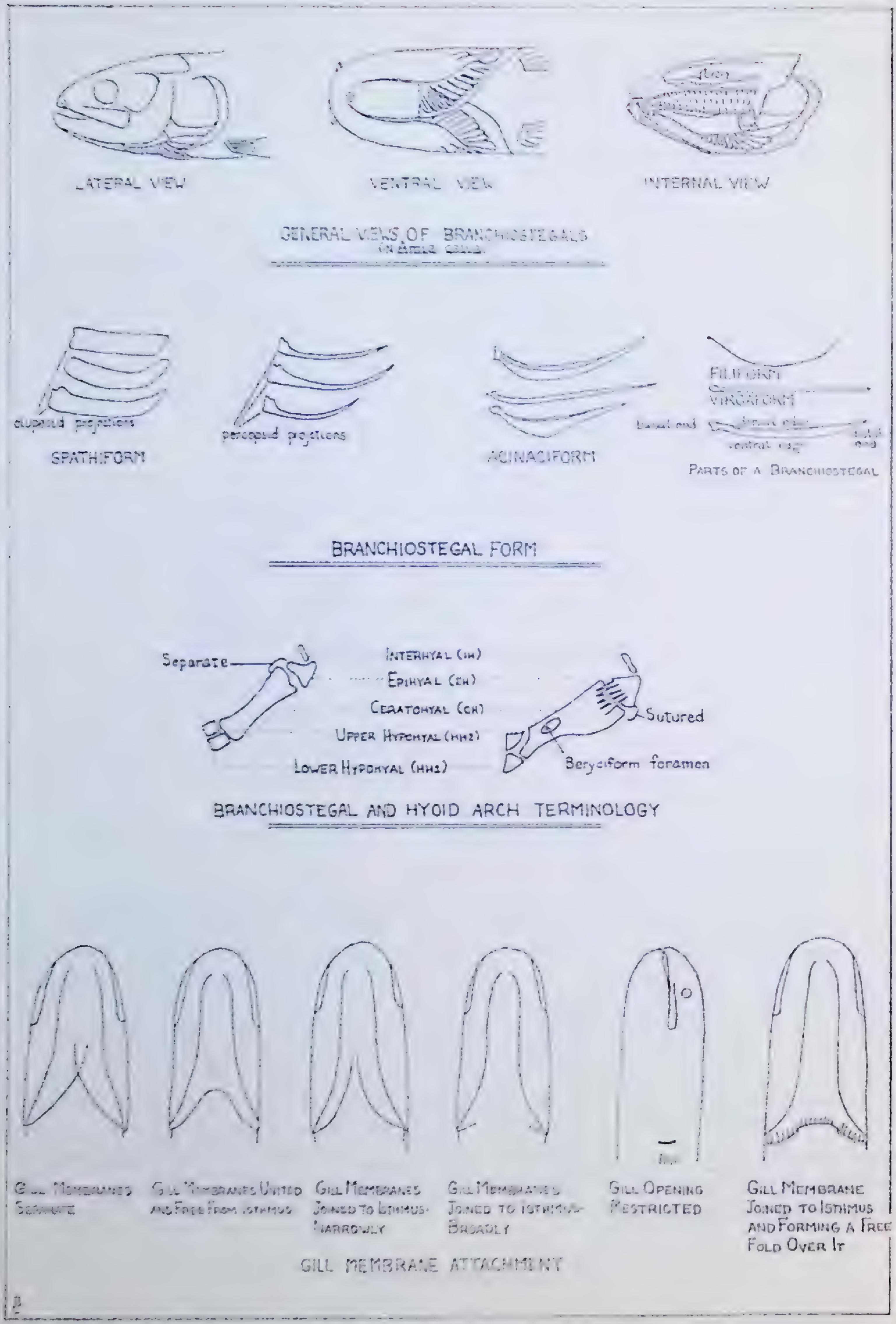

Figure 1. Structural details and relationships of the branchiostegals, hyoid arch, and gill membranes.

and Jordan, have included branchiostegals in their descriptions and analyses of fishes, as have Gill, Ryder, and Starks in their osteological studies.

There have been few studies of branchiostegals on a broad scale. However, Bertelsen and Marshall (1956) discuss the number and arrangement of branchiostegals in some of the malacopterygian orders in connection with the placing of the Miripinnati. Jarvik (1963) reviews the intermandibular bones of some early teleostomes. The only other study, and the most important one, is that of Hubbs (1920). This concise paper enumerates many of the important evolutionary changes in the branchiostegals of living fishes. Hubbs noted the tendency for decrease in branchiostegals during evolution and the differences in shape and arrangement of the branchiostegals of malacopterygians and acanthopterygians. He noted the malacopterygian nature of the branchiostegals in the Synentognathi and the acanthopterygian nature of the branchiostegals in the Microcyprini, Symbranchia, and Opisthomi. He examined about 140 families and more than twenty orders. He gave no figures, and he described only a few forms in detail.

The hyoid arch in fishes has received little attention from the broad comparative point of view. Although Corsy (1933) studied the evolution of the hyoid arch of vertebrates, only a small portion of this study was devoted to teleostome fishes. Khanna (1961) described the hyobranchial skeleton of some Indian fishes. Allis (1915, 1928) and Edgeworth (1926, 1931) comment on the lower elements in discussions on the homologies of the hyomandibular. Woskoboinikoff (1932) comments on the branchiostegal series and hyoid arch in a general study of the respiratory apparatus of fishes.

This paper tries to extend these and other comparative studies by the inclusion of fossil groups, by the examination of nearly every order of teleostomes having branchiostegals and of as many families as possible (over half of the living families),[1] by the presentation of data in a consistent style, by the illustration of many forms, and by the interpretation of the data in terms of phylogeny.

DEFINITIONS

To introduce the subject and to clarify the terminology, the technical terms pertinent to the study are defined, synonyms are listed, and structures are illustrated (Fig. 1). The terminology of Harrington (1955) is used, so far as it applies. Starks (1901) may be referred to for the older synonyms. Two terms, spathiform and acinaciform, are introduced for the first time.

Branchiostegals or *branchiostegal rays*. These are the struts of dermal bone (sometimes cartilage) below the operculars that insert on the hyoid arch and support the gill membranes of Teleostomi. The term 'lateral gulars' is sometimes misapplied to the broad branchiostegals of fossil Chondrostei. The branchiostegals are here believed to be homologous with the hyoid rays of Acanthodii and Elasmobranchii (fused into the "opercular plate" of chimaeras).[2]

---

[1] Thirty-six orders, over 245 of the 402 living families, over 335 species, and 700 specimens were examined. Counts are lacking on only 15 living and 30 fossil families (i.e., data, own and literature, are available for 514 of the total of 559 living and fossil teleostome families). All living orders with branchiostegals were examined, except the Mirapinniformes (Miripinnati).

[2] But Jarvik (1963) believes the short branchiostegals below the jaws in rhipidistian Crossopterygians to be mandibular rays. Miles (1965, Acta Zool. 46:234) calls the hyoid rays of Acanthodii branchiostegals, in accord with my view.

Branchioperculum. This is the enlarged uppermost branchiostegal in *Amia*.

Jugostegelia. These are the branchiostegals which are free from the hyoid arch and which overlap with those of the other side, found in the anguilliform families Echelidae, Ophichthidae, and Neenchelyidae.

Spathiform. Applies to the broad, laminar, paddle-shaped branchiostegals found in chondrosteans, holosteans, and some malacopterygians. From the Latin *spatha* or spatula, e.g., branchiostegals of *Amia*.

Filiform. Applies to string or thread-like branchiostegals. From the Latin *filum* or thread, e.g., most eels.

Acinaciform. Applies to the slender, non-laminar, sword- or scimitar-like branchiostegals found in some malacopterygians and most acanthopterygians. From the Latin *acinaces* or scimitar, e.g., branchiostegals of *Perca*.

Virgaform. Applies to rod-like branchiostegals such as in mormyrids. From the Latin *virga* or rod.

Operculum. The large, dermal, bony (sometimes cartilaginous) upper element of the gill cover behind the preoperculum and inserting on the hyomandibular in teleostomes. Believed to be an enlarged branchiostegal.

Suboperculum. The medium-sized, dermal, bony (sometimes cartilaginous) gill cover element below the operculum in teleostomes. Believed to be an enlarged branchiostegal.

Interoperculum. The medium-sized, dermal, bony (sometimes cartilaginous) element below the suboperculum and the lower arm of the preoperculum and generally partially anterior to the suboperculum. It typically is connected to the mandible, epihyal, and suboperculum. Believed here to be an enlarged branchiostegal. Found only in higher teleostomes (Group II and above).

Accessory operculum. Bone(s) partially or completely intervening between the operculum and suboperculum in some palaeonisciforms. Believed by Gardiner (1963) to be homologous with the operculum and suboperculum, e.g., Cheirolepidae, Rhabdolepidae, Cosmoptychiidae.

Operculars. Collective term for the operculum, the suboperculum, and, if present, the interoperculum.

Gill membrane or *branchiostegal membrane*. The membrane lying between the operculars and the isthmus, which is supported by the branchiostegals. The operculo-gular membrane includes the branchiostegal membrane. The gill membranes may be variously connected to the isthmus. If the gill membranes are not connected to one another nor to the isthmus and if they overlap anteriorly, they are termed *separate* (e.g., Salmonidae, Sphyraenidae). If the gill membranes are attached to one another but not joined to the isthmus, then they are said to be *united and free from the isthmus* (e.g., Polyodontidae, Notopteridae); they may in this case have a small or large free border posteriorly (whether the posterior edge is free may be determined by running a needle under it). In the Synbranchiformes the gill openings are united and free from the isthmus but dorsally attached to the body before the pectoral fin; this gives the appearance of a single ventral gill opening, but it is really only a special case of being united and free. Lastly, the gill membranes may be *joined to the isthmus* (e.g., most Cyprinidae, Gobiidae). They may be *narrowly joined to the isthmus* (e.g., *Gasterosteus*) or joined to the isthmus anteriorly in which case the gill opening is wide, or they may be *broadly* *joined to the isthmus* (e.g., most Cyprinidae) in which case the gill opening is narrow and the space between the gill openings is wide, or the gill opening may be *restricted* (e.g., Anguillidae), in which case the gill opening is reduced to a small aperture. When the gill membranes are joined to the isthmus, a fold may form across the isthmus between the gill slits (e.g., *Myoxocephalus polyacanthocephalus*) which secondarily resembles the gill membranes' united and free condition. The preceding terms have not been used consistently by some authors, but the definitions and illustrations given here should make the distinctions clear and should help standardize the terminology.

Median gular. A median bony plate extending backwards from the symphysis between the mandibles. It is bordered posteriorly by the lateral gulars or branchiostegals (if present). Primitively it bears a V-shaped pit line. It may be derived from the branchiostegals (e.g., *Amia, Elops*). A second median gular, posterior to the normal median gular, is found in some Dipneusti.

Lateral gulars. The pair(s) of bony plates, larger than the branchiostegals, lying between the median gular and the branchiostegals (when present) and inserting on the hyoid arch medial to the mandibles. They are believed here to be homologous with the branchiostegals. Primitively they bear a transverse pit line (e.g., *Polypterus, Calamoichthys, Latimeria*). In some Dipneusti, there may be two pairs, an anterior and a posterior. The term lateral gulars has been misapplied by some authors to the broad branchiostegals of fossil Chondrostei.

Gulars. Collective term for median and lateral gulars.

Branchiostegal series. Collective term for the operculars, branchiostegals, and gulars (all branchiostegal derivatives) (Hubbs's term, *opercular series,* does not include the gulars).

Hyoid arch. Restricted in this study to include only the interhyal, epihyal, ceratohyal, and hypohyals (since the other hyoid elements, the hyomandibular and basihyal (= glossohyal), were not examined and did not bear branchiostegals). They are paired.

Interhyal. Endochondral bony or cartilaginous, usually cylindrical element in teleostomes connecting the lower portion of the hyoid arch to the hyomandibular. It acts as a pivot. It may or may not be homologous with the tetrapod stylohyal (a term which has been used for it). The interhyal typically inserts on the lower tip of the hyomandibular.

Epihyal. Endochondral bony or cartilaginous, usually triangular element in higher teleostomes (Groups II and III) lying between the ceratohyal and the interhyal. Probably derived from the ceratohyal. Since the epihyal does not correspond phylogenetically or embryologically to the epal element, some authors (e.g., Patterson, 1964; Bertmar, 1961) call both the epihyal and the ceratohyal "ceratohyals." The author follows for the moment the majority of authors, including Harrington (1955) and the *Traité de Zoologie* (1958), in calling it the epihyal. It also receives this name in herpetology (Peters, 1964).

Ceratohyal. Endochondral bony or cartilaginous, usually hourglass-shaped element in teleostomes lying between the epihyal, if present, or the interhyal and the hypohyal(s). Found in Acanthodii, Elasmobranchii, and Teleostomi.

Hypohyal (s). Endochondral bony or cartilaginous element(s) lying below the ceratohyal and lateral to the glossohyal in Acanthodii and Teleostomi. In the Crossopterygii, Dipneusti, and lower Actinopterygii (Groups I and II) the hypohyal is single; in the higher Actinopterygii (except where secondarily degenerate) there are a lower (hypohyal 1) and an upper (hypohyal 2) hypohyal. Called basihyals by some authors.

Sutured. The epihyal and ceratohyal are termed *sutured* if they are joined by interdigitating prongs emitted by each bone, and they are termed *separate* if they are not so joined.

Clupeoid projection. This is a bulge which broadens the anterior edge of the base of branchiostegals in clupeoids and their derivatives. *Percopsoid projection* is an angulation on the anterior base of the fourth branchiostegal (*see* Fig. 1).

The *percopsoid projection* is found in certain fishes with little protrusibility of the upper jaw. These fishes depend on inhaling their prey by rapid inflation of the bucco-branchial cavity. The projection gives greater leverage to the muscles that erect the branchiostegals and enlarge the branchial cavity.

Beryciform foramen. This is a perforation above the midsection of the centre of the ceratohyal found in the beryciforms and some of their derivatives. In some fishes the roof of the foramen is lost and only a notch appears on the dorsal edge of the ceratohyal. The foramen perforates the groove along which the hyoid artery runs on the outer face of the ceratohyal. The foramen usually lies above a longitudinal ridge or thickening. Presumably the foramen in leptolepid ceratohyals is a parallelism.

Positional terms. Since the hyoid arch may be almost horizontal or almost vertical, the branchiostegals towards the interhyal end of the arch may be called either the dorsal or the posterior branchiostegals. The branchiostegals toward the hypohyal end of the arch may similarly be called either the ventral or the anterior branchiostegals. In numbering the branchiostegals the uppermost (or posteriormost) provided the starting point since the lower (anterior) branchiostegals are the most variable and do not provide so stable a point of enumeration. The portion of the branchiostegal inserting on the hyoid arch is termed *basal*, and the opposite end is called the *distal tip*. The two long edges may be called the ventral (anterior) edge and the dorsal (posterior) edge. According to the element they insert on, the branchiostegals may be divided into epihyal and ceratohyal (sometimes interhyal and hypohyal) branchiostegals. According to the face of the hyoid arch they insert on, they may be called external, ventral, or internal branchiostegals. When a branchiostegal straddles the epihyal-ceratohyal or a ceratohyal-hypohyal joint one-half a branchiostegal is awarded to each (recorded in descriptions and tables as '½').

CLASSIFICATION

The basis of the classification used herein is that of Berg (1947, 1955). This classification was brought up to date using later literature, such as the *Traité de Zoologie* (1958). Changes, sometimes considerable, were also made in the current classification of living fishes, mainly in the rearrangement of order and status of certain groups, as suggested by this study and data from other studies. The more recent synonyms, particularly those not in Berg, are enclosed in parentheses following the current name. The uniform -iformes ending was adopted for orders, -oidie for suborders, -oidea for superfamilies, -idae for families, and -inae for subfamilies. (The last three are in accord with the Code of Zoological Nomenclature.) The † symbol is used to indicate taxa which are known only from fossils.

Arrangement

The text is presented in phylogenetic order with the most primitive groups first, in so far as this is possible in a linear series. Findings are summarized in the Summary and Conclusions with page references to the pertinent sections in the text.

Not all groups are treated equally. Since data on the fossil groups were obtained from the literature rather than from specimens, wholly fossil groups are described only at the ordinal level (more detailed treatment was accorded in McAllister, 1964). Since there is little variation in the branchiostegals of Perciformes, they were treated at the subordinal level. But the variation in branchiostegals and the number of genera the counts are based on are given for each fossil or perciform family, e.g., 10–11/5 means 10–11 branchiostegals in the five genera examined. In all groups parentheses are used to indicate rare branchiostegal counts, e.g., 5–7(8) means counts of 5 to 7 are common, those of 8 rare. In the groups other than fossils or perciforms descriptions are given at the family level. At least one illustration of every order is given.

Following the descriptions of the branchiostegal series and hyoid arch of each group, the papers referred to for data to supplement the author's observations are listed. Then a list of the material examined is given. Well over 500 publications were examined for branchiostegal or hyoid arch data. Because of the numerous taxa treated and despite the consultation of many taxonomic papers, some groups may have incorrect names or names which do not agree with the latest revision. The author hopes the reader will tolerate these lapses and inform him of them.

Methods

The branchiostegal series and the hyoid bones were examined by several methods. The principal method was by clearing and staining with alizarin following the method of Hollister (1934). Specimens preserved in alcohol, usually from three to six inches in length but sometimes as short as one inch (Phallostethidae) or as long as sixteen inches, were employed for staining. The stained hyoid arch with the branchiostegals usually was removed and examined. Some were photographed under a binocular microscope. In quite a few cases dermestid-cleaned skeletons were examined; caution was necessary since branchiostegals may be lost during skeletonizing. Some alcoholic specimens were dissected for examination of the arch and the branchiostegals. From other alcoholic specimens branchiostegal counts were taken without dissection. In the latter method it is important to determine whether the uppermost branchiostegal is hidden under the suboperculum and whether the lowest branchiostegal, which may be quite small, is obscured by the skin. An attempt was made to examine at least one specimen per family (sometimes up to 50) from as many families as possible. Examination was usually supplemented from the literature. Representatives were chosen by availability except that as many families and suborders as possible were examined.

Branchiostegals were counted on the left. When the branchiostegals were abnormal (e.g., fused, bent, or irregularly placed; *see* Crossman, 1960, for examples) the counts were not recorded.

The principal sources of material were the National Museum of Canada, Ottawa (NMC), and the museum of the Institute of Fisheries, University of British Columbia (BC). Other material was borrowed from Stanford University (SU), the Royal Ontario Museum (ROM), the British Museum (BM), Scripps Institution of Oceanography (SIO), and the University of Michigan Museum of Zoology (UMMZ), or examined at the United States National Museum (USNM). The acknowledgments note other sources.

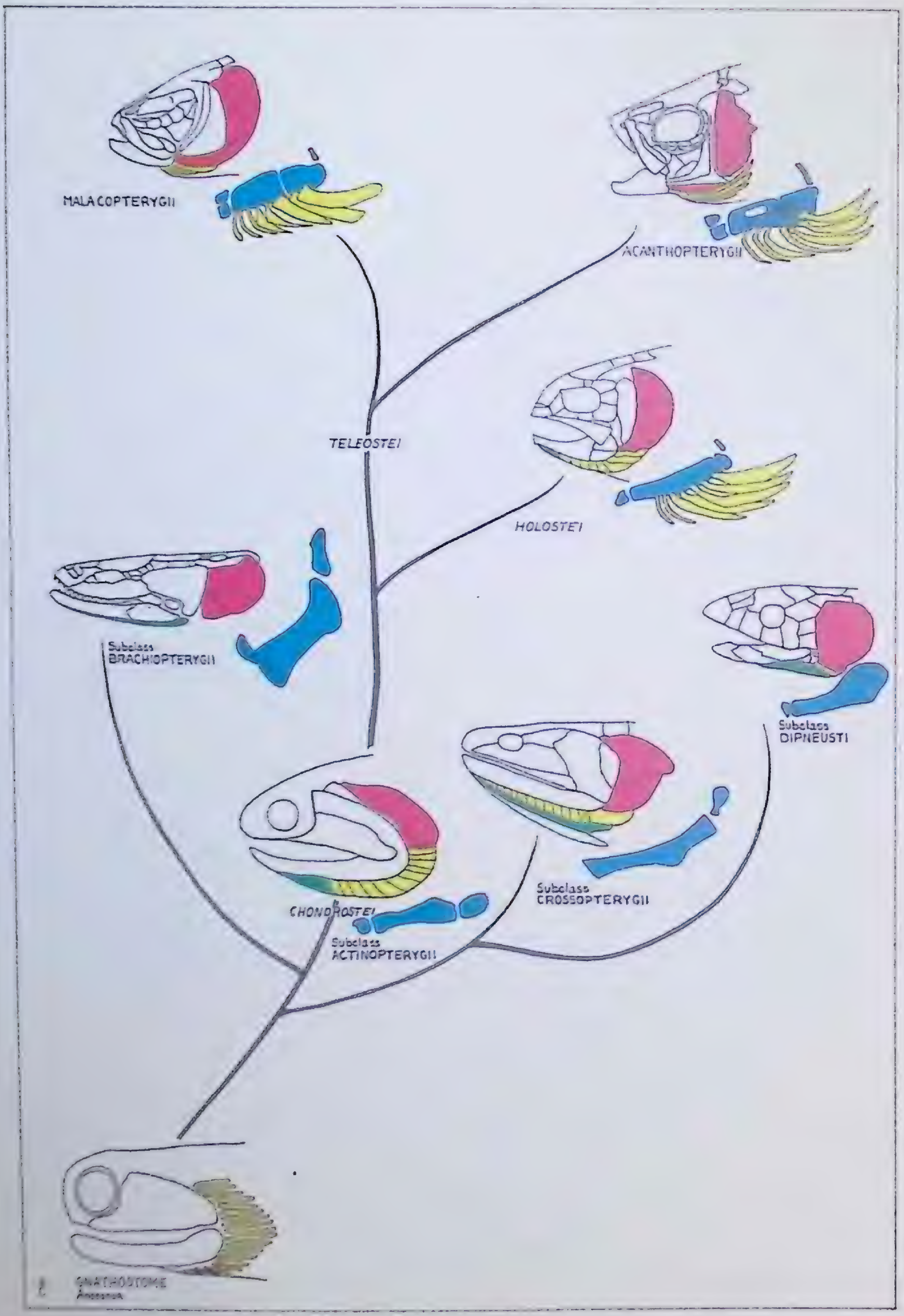

Figure 2. Evolution of the major groups of teleostome fishes showing changes in branchiostegals, operculars, gulars, and hyoid arch.

Class TELEOSTOMI (Including Dipneusti)

Branchiostegals (0–2) 3–20 (21–50). One (or two) median gular(s), one or two pairs of lateral gulars present or absent. Operculum, suboperculum, and (in higher groups) interoperculum usually present. Interhyal, epihyal (in higher groups), ceratohyal, and one or two (in higher groups) hypohyals usually present but sometimes lost. Lower Devonian to present. Four subclasses and 69 orders, 39 of which are living.

Although the subclass Actinopterygii is considered more primitive than the Crossopterygii, Dipneusti, and Brachiopterygii, the latter are placed first because they are more primitive than the higher Actinopterygii. The Brachiopterygii might best be placed as a chondrostean order of the Actinopterygii. But until its affinities are known with greater certainty it would appear preferable to leave it in a separate subclass.

The Dipneusti are often included in the same class as the other bony fishes, but Berg isolated them as a class. Since the Dipneusti are derivable from the Crossopterygii and since they are not distinguished to a higher degree than the other subclasses of teleostomes, they are included in the Teleostomi, not in a separate class.

Of the four subclasses, the Actinopterygii appear most primitive. Their branchiostegals are most numerous and their lateral gulars, in primitive members, are little differentiated in size from neighbouring branchiostegals. The Crossopterygii and Dipneusti are more advanced in that they have fewer branchiostegals and enlarged lateral gulars. Primitively, and in contrast to the Actinopterygii, these two subclasses also share one or more branchiostegals marked by pit lines. Advanced members may lose the pit lines. It is suggested that the Crossopterygii arose from the Actinopterygii or its ancestors. The Dipneusti, which have few or no branchiostegals and modified lateral gulars, probably arose from the Crossopterygii or their ancestors. The Brachiopterygii probably arose from moderately advanced chondrostean Actinopterygii. (*See* Fig. 2 for illustration of relationships.)

Subclass Crossopterygii

Branchiostegals 0–13, one with or without a pit line; median gular present or absent, primitively with a V-shaped pit line; a single pair of large gulars at least two-thirds the length of the mandible; an operculum present and usually a suboperculum; interhyal, ceratohyal, and hypohyal present. Lower Devonian to present. Two superorders with three orders and ten families.

†Superorder Osteolepides (Rhipidistia)

Branchiostegals present; median gular present or absent. Lateral gulars taper along their whole length towards the anterior tip. Suboperculum ventral to operculum and taking normal part in movement of gill cover. Lower Devonian to Upper Carboniferous. Two orders. (*See* Note 1, Addenda.)

Thomson (1962, 1964) considers the differences between the groups of Osteolepides to be overstated and, contrary to Jarvik and Berg, suggests division into three superfamilies of equal rank—Hoploptychoidea, Osteolepoidea, and Rhizodontoidea. Jarvik (1963) retains the two orders; he considers the short branchiostegal rays below the jaw in osteolepiforms and porolepiforms to be mandibular rays rather than branchiostegal rays.

†Order **POROLEPIFORMES (HOPLOPTYCHIFORMES)**

Pl. 1

Branchiostegals 10–13, the first 4–6 long and below the suboperculum, the other 4–9 short and below the jaws; median gular apparently absent; a large pair of gulars with an arc-shaped pit line; operculum and suboperculum present; lower edge of suboperculum on upper edge of third preoperculum. Lower to Upper Devonian.

Two families are included: †Porolepidae—no data available; †Hoploptychidae 10–13/1.

References. Jarvik (1948, 1963), Stensio (1947), Woodward (1891).

†Order **OSTEOLEPIFORMES (RHIZODONTIFORMES)**

Pl. 1

Branchiostegals 4–8; usually a median gular with pit line; one pair of large lateral gulars with pit line; suboperculum with lower edge not on upper edge of third preoperculum; operculum and suboperculum present. Middle Devonian to Lower Permian.

Taxonomy. The operculars, gulars, branchiostegals, and other skull bones of Rhizodontiformes are so similar in form and arrangement that I feel compelled to return this order to the Osteolepiformes, following Arambourg (1958).

Four families are included: †Gyroptychiidae 6–8/1; †Osteolepidae (Parabatrachidae) 4–7/2; †Eusthenopteridae 8/1; †Rhizodontidae 5/1.

References. Berg (1947, 1955), Bryant (1919), Jarvik (1944, 1948, 1952, 1963), Traquair (1883), Woodward (1891).

Superorder **Coelacanthi (Actinistia)**

Branchiostegals and median gular absent. Lateral gulars of even breadth, tapering only at tips. Suboperculum at least partially opposite lower portion of operculum and apparently not taking part in movement of gill cover. Middle Devonian to present. One order.

Order **COELACANTHIFORMES**

Pl. 1

A large pair of lateral gulars of even breadth bearing an arc-shaped pit line. Suboperculum at least partially opposite lower portion of operculum. Suboperculum apparently not taking part in movement of the gill cover. Interhyal and ceratohyal present. Middle Devonian to present.

Taxonomy. There are no notable differences in the branchiostegal series among the three suborders of Coelacanthiformes. Arambourg (1958) does not employ the suborders in his classification.

Relationship. The Coelacanthiformes are more similar to the Osteolepiformes than to the Porolepiformes in that the suboperculum is next to the third preoperculum, in that the branchiostegals are fewer in Osteolepiformes, and in that the sensory canals of the head, as portrayed by Stensio (1947), are of a more similar pattern.

Three suborders with four families are included; only one living family: †Suborder Diplocercidoidei: †Diplocercidae; †Suborder Laugioidei: †Laugiidae; Suborder Coelacanthoidei: †Coelacanthidae, Latimeriidae.

References. Echols (1963), Gardiner (1960), Goodrich (1909), Lehman (1952), Millot and Anthony (1959), Moy-Thomas (1937), Schaeffer (1952), Smith, J. L. B. (1940), Stensio (1921, 1932, 1947), Zittel (1887).

Subclass **Dipneusti (= Dipnoi)**

Branchiostegals three or less; median gular present or absent; 1–2 pairs gulars present or absent (combined length of lateral gulars exceeds one-half mandible length); operculum and suboperculum present; a hypohyal present or absent; a ceratohyal always present; an interhyal may be present. Late Early Devonian to present. The dipneustians are divided into two superorders—the Dipteri and the Ceratodi—six orders, and twelve families.

The Ceratodi have a complete branchiostegal series and full-sized operculars, whereas the Dipteri have lost the gulars and branchiostegals and have reduced operculars. The Dipteri are readily distinguished from other fishes by their greatly expanded pentagonal operculum, and the Ceratodi are distinguished by their very reduced operculum. The differences in the branchiostegal series alone certainly justify the separation of the Ceratodi and the Dipteri. The differences between the two indeed make it difficult to characterize the subclass Dipneusti as a whole. However, the differences should be not unduly weighted since they are concerned mainly with a loss or reduction in characters.

The suboperculum rests solely on the ceratohyal, unlike other fishes in which it usually rests on the hyomandibular or preoperculum. Further, the suboperculum is much more slender than in other teleostomes, except in *Scaumenacia.* It might therefore be questioned whether or not the dipneustian subopercle is a branchiostegal. However, the condition of the suboperculum in *Scaumenacia,* where it is of normal size and shape, would seem to oppose this thesis. Further, the unusual insertion of the suboperculum may be accounted for by the supposition that the great expansion of the operculum in the Dipteri has necessitated a lower insertion of the suboperculum; it has been displaced down from the hyomandibular to the ceratohyal. This position has been conservatively retained in the Ceratodi even though the size of the operculum has been reduced.

The possession of branchiostegals, operculum, suboperculum, median and lateral gulars by primitive dipneustians shows clearly that they are related to the other subclasses of teleostomes. But when they first appear in the fossil record they are already quite specialized; most branchiostegals are already lost; the gulars are more modified than in primitive representatives of the other subclasses; and the operculum is considerably enlarged. Although these features distinguish them, they certainly do not warrant the distinction of the dipneustians as a class. The many similarities to the primitive members of the other teleostome subclasses confirm their placement together in a single class.

The arrangement of branchiostegals and gulars in primitive dipneustians enables them to be derived from primitive Crossopterygii, but not vice versa. This opinion is in agreement with Westoll (1949) who believes either that the Dipnoi stemmed from the Rhipidistia or that both groups have a common ancestor. To the points listed by Westoll for such a common ancestor the following may be added: a median gular, a pair of lateral gulars with a pit line, and broad short branchiostegals.

†Superorder **Dipteri**

Branchiostegals present in at least Dipteriformes and Phaneropleuriformes. Gular plates present (unknown in Uronemiformes). Operculum large, roughly pentagonal. Ceratohyal present. Middle Devonian to present. Four orders.

†Order **DIPTERIFORMES (RHYNCHODIPTERIFORMES)**

Pl. 2

Branchiostegals 2–3; a small median gular; 1–2 pairs of lateral gulars, the posterior bearing pit lines; a large pentagonal operculum and a small elongate suboperculum present. Late Early Devonian to Upper Devonian.

Three families are included: †Dipnorhynchidae 2/1; †Rhynchodipteridae—no data available; †Dipteridae 3/1.

References. Graham-Smith and Westoll (1937), Hills: (1933), Save-Soderbergh (1937), Watson and Gill (1923), Westoll (1949).

†Order **PHANEROPLEURIFORMES**

Pl. 2

Branchiostegals two; a small median gular and two large pairs of gulars present; a large operculum and medium-sized suboperculum present; ceratohyal present. Upper Devonian.

Three families: †Phaneropleuridae—no data available; †Scaumenacidae 2/1; †Fleurantiidae—no data available.

References. Graham-Smith and Westoll (1937), Stensio (1947), Whiteaves (1889), Woodward (1891).

†Order **URONEMIFORMES**

Branchiostegals and gulars not known; a large oval operculum and a small elongate suboperculum present; ceratohyal present. Lower Carboniferous to Upper Permian.

Taxonomy. Romer does not distinguish the Uronemidae from the Dipteridae. Arambourg and Guibe synonymize the Conchopomidae with the Uronemidae and the Uronemiformes with the Ctenodontiformes. Berg's classification is provisionally retained here.

Two families are included: †Uronemidae and †Conchopomidae—no data available.

References. Watson and Gill (1923), Woodward (1891).

†Order **CTENODONTIFORMES**

Pl. 2

Branchiostegals not known; one pair of gular plates known; large scallop-shaped operculum; small elongate suboperculum. Lower Carboniferous to Lower Triassic.

One family is included: †Ctenodontidae—no data available.

Superorder **Ceratodi**

Branchiostegals and gular plates absent. Operculum reduced to an elongate ray which rests on the supratemporal-intertemporal (squamosal). The slender suboperculum rests on the ceratohyal. Ceratohyal and sometimes hypohyal present. Interhyal absent except in larvae. Upper Carboniferous to present. Two orders.

Taxonomy. Arambourg and Guibé (1958) synonymize, without discussion, the Lepidosireniformes with the Ceratodiformes. These two orders are retained here; hyoid arch differences suggest their separation.[1] The Ceratodiformes appear to be more primitive in that the operculum is less reduced and the posterior end of the ceratohyal is normally expanded.

Order **CERATODIFORMES**

Pl. 2

A reduced operculum and suboperculum present; hypohyal, ceratohyal (expanded greatly at the upper end) and interhyal present in larvae. Upper Carboniferous to present. One family which includes a living representative, *Neoceratodus forsteri*, in Australia.

One family is included: Ceratodidae.

CERATODIDAE

Pl. 2

Operculars. In *Neoceratodus* operculum reduced in size and shaped like an arrowhead pointing posteriorly. The elongate oval suboperculum inserts on the expanded distal end of the ceratohyal. Under the distal end of the suboperculum is an oval cartilaginous plate. Gill opening restricted to side of head.

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[1] Thomson (1965, Proc. Zool. Soc. London 145: 207–238, 1 pl., 12 text-fig.) states that the structure of the nasal capsule in the *Lepidosiren-Protopterus* stock differs greatly from that of the *Neoceratodus* stock.

Hyoid arch. Composed of a small rectangular cartilaginous hypohyal and a large ossified ceratohyal. The ceratohyal is shaped as in Conchopomidae, that is, of even breadth anteriorly, and expanded greatly at its posterior end. Figures in Gregory, Goodrich, and Holmgren and Stensio show no other hyoid bones (except a small cartilaginous hyomandibular). De Beer shows three bones—the "stylohyal," the ceratohyal, and the hypohyal—in a larval specimen. In the adult specimen here examined only a ceratohyal was present; the cartilaginous hypohyal, if present, was shrivelled, and there was no sign of an interhyal.

References. de Beer (1937), Goodrich (1958), Gregory (1951), Holmgren and Stensio (1936), Ridewood (1894).

Material examined. Neoceratodus forsteri, skeletal specimen, uncatalogued NMC, Queensland, Australia.

Order **LEPIDOSIRENIFORMES**

Pl.2

Operculum and chevron-shaped suboperculum reduced to slender rays; only the ceratohyal (slightly expanded at the upper end) present in hyoid arch. Two families are included; Lepidosirenidae with a single living species in Brazil, and Protopteridae with four living species in Africa. Upper Carboniferous to present.

LEPIDOSIRENIDAE

Pl. 2

Operculars. Operculum reduced to an elongate flat ray bearing a small cartilage under its distal tip in *Lepidosiren.* It inserts on the supratemporal-intertemporal (squamosal), the hyomandibular being absent. The suboperculum is shorter but wider than the operculum. The suboperculum is chevron-shaped and inserts on the upper ceratohyal. It is underlain by a broader cartilaginous base. This base is called an interoperculum by Bridge, but it can hardly be that bone which is unknown in the dipneustians (found only in the more advanced Actinopterygii). Nor are the cartilaginous distal tips of the operculum and suboperculum likely to be remnants of a hyoid ray, as he suggests; they are unossified portions of the operculum and suboperculum. Gill opening restricted to side of head.

Hyoid arch. Only a ceratohyal is present (even embryologically), the hypohyal, interhyal, and hyomandibular being absent. The ceratohyal is large, bowed slightly downwards, and expanded slightly at each end. It is attached to the parasphenoid by a ligament (the hyomandibular being absent). There is an odd patch of cartilage on the outer surface of the distal portion of the ceratohyal.

References. de Beer (1937), Bridge (1898), Gregory (1951), Holmgren and Stensio (1936), Ridewood (1894).

Material examined. None.

Operculars. The operculum tapers posteriorly to a point in *Protopterus*; it appears to insert on the supratemporal-intertemporal (squamosal). The operculum bears an inner cartilage as in *Neoceratodus.* The suboperculum is essentially similar to that in *Lepidosiren*, being an elongate chevron-shaped bone over a cartilaginous base. It inserts on the posterior end of the ceratohyal. Gill opening restricted to side of head.

Hyoid arch. Only a ceratohyal is present; the basihyal, hypohyal, interhyal, and hyomandibular are lacking. The ceratohyal is large and is slightly expanded at each end. There is a patch of cartilage on the outer surface of the anterior end of the ceratohyal. Although this is called a vestigial hyoidean ray by Bridge, its position does not confirm this suggestion. Ligaments connect the ceratohyal to the skull and to the lower jaw, as in *Lepidosiren.*

Relationship. The correspondence of the operculars and the ceratohyal in Lepidosirenidae and Protopteridae suggests that they are closely related.

References. Bridge (1898), Dean (1895), Ridewood (1894).

Material examined. None.

Subclass Brachiopterygii

Order POLYPTERIFORMES

Pl. 3

Branchiostegals absent; median gular absent; a very large pair of lateral gulars (longer than two-thirds of mandible length); large operculum; small suboperculum present or absent; interoperculum absent. Interhyal, ceratohyal, and hypohyal present. Lower Tertiary (Eocene) to present. A single order and family.

It is the only group derived from the actinopterygians having lateral gulars and lacking branchiostegals. The absence of an interoperculum relates it to the lower Actinopterygii. The enlarged lateral gulars recall those of *Pyritocephalus* and *Haplolepis* (Haplolepiformes). These forms also have pit lines on the lateral gulars, reduced branchiostegals, and larger operculum than suboperculum. The similarity of the lateral gulars to those of the Crossopterygii and Dipneusti is doubtless a parallelism. The lateral gulars have expanded and cover the region exposed by the loss of the branchiostegals.

Evidence on the relations of the Brachiopterygii also comes from its sensory lines (Stensio, 1947). The sensory line of the cheek is of the actinopterygian type. In its principal features it is much the same as in advanced lower ganoids, but in some respects it has reached the stage of holostean ganoids. The postmaxillary line is similar in its connection with the dermal bones to lower ganoids and parasemionotids. They are probably derived from some subholostean ancestor (Stensio, 1947). Pehrson (1947) interprets the skull bones as indicating actinopterygian affinity. Recent evidence on relationships has come from a serum protein study. De Bont and Paulus (1964) found that the serum protein pattern of *Polypterus* showed a striking resemblance to that of all the teleosts studied and no resemblance at all to that of *Protopterus.*

POLYPTERIDAE
Pl. 3

Branchiostegals. Absent.

Gulars. Median gular absent. A pair of large lateral gulars which extend from the symphysis to slightly past the posterior end of the mandibles, extending in the midventral line to a point just before the posterior end of the mandibles. A short transverse pit line in the form of an arc is found near the middle of each lateral gular. In *Calamoichthys* the gulars are slightly shorter, and the tip of the right overlaps the tip of the left. The large gular plates are reminiscent of those in Crossopterygii.

Operculars. In *Polypterus* the operculum is oval and larger than the triangular suboperculum. Suboperculum absent in *Calamoichthys*. Gill membranes separate, with right over left.

Hyoid arch. A partially ossified hypohyal, a ceratohyal, and an interhyal are present. The ends of the ceratohyal and interhyal are not ossified.

Taxonomy. The family Polypteridae consists of two living African freshwater genera, *Polypterus* and *Calamoichthys* (= *Erpetoichthys*).

References. Allis (1922), Berg (1947), Daget (1958), Devillers (1958).

Material examined. Calamoichthys sp., alcoholic specimen, ROM 18877, Nigeria.

Subclass Actinopterygii

Branchiostegals 0–50; median gular present or absent, primitively with a V-shaped pit line; lateral gulars, if present, with length less than one-half of mandible length; operculum and suboperculum usually present; in higher forms an interoperculum usually present; interhyal, epihyal (in higher forms), ceratohyal, and hypohyal(s) usually present. Lower Devonian to present. Five supraordinal groups with 60 orders, 36 of which are living.

It has been made apparent by various authors, such as Stensio, Berg, Schaeffer, and Gardiner, that the Chondrostei, Holostei, and Teleostei (as they have been constituted) were not natural groups, that the Holostei were polyphyletic, and that some of the characters used to distinguish the Holostei occurred in certain chondrosteans.[1] These factors have been interpreted as meaning that the Chondrostei, Holostei, and Teleostei were not valid groups, and that their names should be dispensed with.

However, another interpretation is possible, that the groups should be modified and retained. First, some orders have been placed in the wrong group. Secondly, some of the characters previously used to define the groups have not been diagnostic, although they may tend to be more frequent in one group than another. According to this interpretation the groups, if reconstituted and redefined, would be natural and valid. This interpretation is discussed below.

The interoperculum is an important character in diagnosing the Holostei. It is absent in all the Chondrostei and present in the Holostei and Teleostei (except in a few groups where it is secondarily lost). One group presently placed in the Holostei, the Lepisosteiformes, lacks an interoperculum but has a maxillary free from the cheek. However, the jaws have moved forward decreasing the need for an interoperculum, and the preoperculum has expanded ventrally supplanting the position normally occupied by an interoperculum. The possession of a rostral and the position of the nostril show that the genetic affinities of the Lepisosteiformes lie with the holosteans (Gardiner, 1963). It may safely be said, therefore, that the interoperculum has been lost and that the Lepisosteiformes belong in the Holostei.

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[1] Gosline (1965, Copeia (2):186–194) discusses views of some of the authors who consider these groups polyphyletic.

The Platysiagiformes have been placed among the advanced Chondrostei—in the subholostei. However, they possess a definite interoperculum (Gardiner, 1960), a coronoid process, and a rostral (but a fixed maxilla). These and subsidiary characters, such as the fin ray – basal relationship, lack of a clavicle, and lack of lateral gulars, clearly indicate that it should be placed in the Holostei, not in the Chondrostei.

Brough (1939) considered the Luganoiidae to be subholostean. But the maxilla of *Luganoia* is free, and there is a coronoid process on the mandible. Brough (1939) thought that the interoperculum was absent. But it actually appears from his paper that the portion of the head including the branchiostegals was not preserved. An interoperculum may therefore have been present. Because of the aforementioned two positive holostean characters I place the Luganoiiformes amongst the Holostei.

The Ospiiformes have been considered chondrosteans, but their maxillary is free and it is now clear that they possess an interoperculum (Stensio, 1932; Lehman, 1952). Further, they possess an independent rostral element which is unknown below the ospiid level of organization (Gardiner, 1963). There now appears to be good reason to place the Ospiiformes in the Holostei.

The Pycnodontiformes lack an interoperculum and yet have been placed in the Holostei by previous authors. But some recent authors (Rayner, 1941; Gardiner, 1960) and myself are in agreement as to their placement in the chondrosteans near the platysomoids or bobasatraniiforms.

When the above changes have been made the Chondrostei and the Holostei comprise homogeneous groups. All the Holostei have a free maxillary and an interoperculum (except that the maxilla is fixed in the Platysiagiformes and that the interoperculum is lost in the Lepisosteiformes), and all the Chondrostei have a fixed maxillary (except *Dorypterus* where the maxillary has shortened and become secondarily free) and lack an interoperculum. That there are other characters which would support this grouping is suggested by Schaeffer's fine association analysis of differential characters. It is also certain that some characters, previously employed to characterize the groups (such as the relation of median fin rays to their supports or the form of the caudal fin), do not definitively separate the two groups. (However, it might still be possible to state that in chondrosteans fin rays exceed or equal the pterygiophores and in holostei they equal the pterygiophores.)

The following synopsis summarizes my understanding of these three groups. In characterizing these groups it must be remembered that an order may lose one of the characters of its group. Although the rare loss of a character would invalidate its use in keys, it is not fatal to its value in phylogenies. Other characters will show that the group belongs in this phylogenetic position.

GROUP I, *Chondrostei*. Without interoperculum, supramaxillaries, rostral, and coronoid process. May have lateral gulars and clavicles. Maxillary not normally free. Have lepisosteid tubules in scales; but one hypohyal. Interhyal inserts dorsally on symplectic.

GROUP II, *Holostei*. May have interoperculum, supramaxillary(ies), rostral, and coronoid process. Without lateral gulars and clavicles. Maxillary free. Have lepisosteid tubules in scales; but one hypohyal. Interhyal inserts dorsally on hyomandibular.

GROUP III, *Teleostei*. May have interoperculum, supramaxillary(ies), and (rarely) rostral. Coronoid process present or absent. Lack lateral gulars and clavicles. Maxillary free. Lack lepisosteid tubules in scales. Primitively with two hypohyals, secondarily with one or none. Interhyal inserts dorsally on hyomandibular.

Even if authors feel that these definitions are not adequate, it seems clear that the groupings are very close to natural ones. The use of several firm phylogenetic characters with rejection of previously used weak characters and reorganization of the orders has eliminated inconsistencies in the classification.

For the above reasons the modified supraordinal groups Chondrostei[1] (Group I), Holostei (Group II), and Teleostei (Group III) are reinstated. The Teleostei are further subdivided into the Malacopterygii (Group IIIA) and the Acanthopterygii (Group IIIB) (*see* p. 33). The group Mesichthyes is discarded.

Group I. CHONDROSTEI

Without interoperculum. Operculars usually entire. Lateral gulars present or absent. A single hypohyal. Lower Devonian to present. Seventeen orders.

†Order PALAEONISCIFORMES (AEDUELLIFORMES, GYMNONISCIFORMES)

Pl. 3

Branchiostegals (1)4–23, spathiform; median and (in many) a pair of lateral gulars; operculum and suboperculum present, accessory opercular sometimes present (*see* Gardiner, 1963); interhyal, epihyal, ceratohyal, and a hypohyal known. Lower Devonian to Lower Cretaceous. Several families.

Following Lehman (1958), Berg's Gymnonisciformes are included in the Palaeonisciformes. The Palaeonisciformes are a diverse group which will probably be broken up into other orders when a detailed taxonomic revision is made. However, the practice of removing poorly known families from Palaeonisciformes and raising them to ordinal status does not seem advisable.

An intermediate path between Berg's recognition of few palaeoniscoid and

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[1] Gosline (1965, Copeia (2): 186–194) agrees that the Teleostei represent a monophyletic supraordinal group, with the possible exception of the hiodontid osteoglossoid mormyroid line. I also suggest that this group, excepting the hiodontids, may belong amongst the Holosteii.

Obruchev (1964, Osnovi paleontologii. Bescheliostnie, ribi. Moscow, 522 p.) also recognizes the above three groups as superorders. He recognizes, in addition, the superorders Palaeonisci and Polypteri. Their Chondrostei contains the Saurichthyiformes, Errolichthyidae, and the Acipenseriformes.

Romer's many families is followed. Gymnoniscidae (Gymnonisciformes of Berg) is included in Palaeoniscidae following Westoll (1944) and Lehman (1958). The classification of palaeoniscoids herein is not satisfactory and an overall revision is needed.

Two suborders with nineteen families are included: †Suborder Palaeoniscoidei: †Cheirolepidae 11–13/1; †Tegeolepidae 30 or more/1; †Stegotrachelidae 6/1; †Palaeoniscidae[1] (1) 4–23, usually 9–15/15; †Elonichthyidae 6–8/1; †Cosmoptychidae 15–20/2; †Acrolepidae 7–15/4; †Pygopteridae 20/2; †Rhabdolepidae 16/1; †Amblypteridae 7/1; †Centrolepididae ca. 12/1; †Commentryidae—no data; †Coccolepidae 14–15/1; †Birgeriidae 14/1; †Holuridae 8–12/2; †Urosthenidae—no data; †Turseoidae 6–7/1; †Suborder Platysomoidei; †Platysomidae 4–7/2; †Amphicentridae 5–9/3.

References. Aldinger (1937), Berg (1947, 1955), Bock (1959), Brough (1933), Dyne (1939), Gardiner (1960, 1963), Gregory (1951), Lehman (1947, 1952, 1958), Moy-Thomas (1937), Moy-Thomas and Dyne (1937), Nielsen (1942, 1949), Romer (1955), Traquair (1875), Watson (1925) Westoll (1944), White (1933, 1939), Woodward (1891, 1898), Woodward and White (1926).

†Order **TARRASIIFORMES**

Pl. 3

Branchiostegals 15, spathiform; gulars not known, but the broad anterior branchiostegal may be a lateral gular; operculum and suboperculum present. Lower Carboniferous.

A single family is included: †Tarrasiidae 15/1.

References. Moy-Thomas (1934), Traquair (1881).

†Order **PHANERORHYNCHIFORMES**

Pl. 3

A 'long series' of branchiostegals; gulars not known; operculum and suboperculum present; Middle Carboniferous.

A single family is included: †Phanerorhynchidae: a 'long series'/1.

References. Gill and Watson (1923), Stensio (1932).

†Order **HAPLOLEPIFORMES**

Pl. 3

Branchiostegals 1–3, spathiform, the one next to the lateral gular expanded; median and lateral gulars large; V-shaped pit line on median gular; operculum and suboperculum present. Upper Carboniferous.

A single family is included: †Haplolepidae 1–3/2.

References. Lehman (1958), Westoll (1944).

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[1] Includes the families Thrissonotidae (Oxygnathidae), Rhadinichthyidae, Canobiidae, Scanilepidae, Dicellopygidae, Boreolepidae, Cocconiscidae, Gymnoniscidae (Trissolepididae), Cornuboniscidae, Styracopteridae, Aeduellidae (the latter raised to ordinal status in the classification outline in *Traité de Zoologie*, 1958).

†Order **REDFIELDIIFORMES**
Pl. 4

One large spathiform branchiostegal (sometimes divided) below suboperculum, perhaps absent in some; gulars absent; operculum and suboperculum present. Lower to Upper Triassic.

Taxonomy. Dictyopygidae is a junior subjective synonym. *Redfieldius* is a necessary replacement name for *Catopterus* Redfield 1837 (a homonym of *Catopterus* Agassiz 1833). The family name should be based on *Redfieldius* rather than *Catopterus* Redfield. Following Lehman (1958), Brookvaliidae is synonymized with Redfieldiidae.

A single family is included: †Redfieldiidae 1(2)/6.

References. Berg (1955), Brough (1931, 1934), Wade (1935).

†Order **PERLEIDIFORMES**[1]
Pl. 4

Branchiostegals 7–12, spathiform; a median gular with a V-shaped pit line, and a pair of lateral gulars; operculum and suboperculum present; ceratohyal known. Lower to Upper Triassic.

Teleopterina (=*Pyritocephalus*) is included in the Haplolepidae following Westoll (1944). Cleithrolepidae is included in the Perleididae following Lehman (1958).

A single family is included: † Perleididae[1] 7–12/5.

References. Brough (1939), Lehman (1952), Schaeffer (1955), Stensio (1921), Wade (1935).

†Order **DORYPTERIFORMES**
Pl. 4

Branchiostegals, gulars, possibly operculum, and suboperculum absent (although a small bone has been tentatively identified as an operculum in one specimen). Ceratohyal questionably present. Upper Permian.

The reduction in the branchiostegal series suggests derivation from the Platysomoidei rather than from the Palaeoniscoidei. In this character it also approaches the Bobasatraniiformes and Pycnodontiformes.[2]

A single family is included: Dorypteridae 0/1.

References. Berg (1947), Gill (1925), Stensio (1932), Westoll (1941).

†Order **BOBASATRANIIFORMES**
Pl. 4

Branchiostegals, if present, 1–2 or 4; gulars unknown; operculum present; suboperculum absent; a ceratohyal present. Lower Triassic.

A single family is included: †Bobasatraniidae 1–2, or 4 or more/1.

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[1] Obruchev (1964. *See* footnote following page) notes that Colobodontidae Stensio 1916 has priority over its synonym Perleididae. This being so, the ordinal name should be changed.

[2] Obruchev (1964) unites in the order Platysomida the Platysomoidei, the Dorypteriformes, and the Bobasatraniiformes (Osnovi paleontologii. Bescheliostnie ribi, Moscow, 522 p.).

References. Berg (1947), Lambe (1914), Lehman (1958), Stensio (1932), Westoll (1941).

†Order PYCNODONTIFORMES

Pl. 4

Branchiostegals at least 2–5, acinaciform, virgaform, or spathiform; gulars absent; elongate vertical operculum; suboperculum replaced by preoperculum.[1] Upper Triassic to Eocene.

Relationships. The phylogenetic position of this order has been an enigma. Berg and Romer place it among the holosteans, Arambourg and Bertin in their enlarged order Amiiformes. Stensio (1947), until the question of holostean classification has been solved, provisionally retains it in the Holostei. Gardiner (1960) derives it, with the Bobasatraniiformes, from an offshoot of the Dorypteriformes. Rayner (1941) places it in the subholosteans and regards it as derived from the platysomids.

Because of the absence of an interoperculum the order is here placed in Group I. The skull and body structures show similarities to the Dorypteriformes and Bobasatraniiformes. Like the Dorypteriformes and Bobasatraniiformes the Pycnodontiformes have a large ventral preoperculum which replaces the suboperculum; a dorsal preoperculum; no interoperculum; an elongate and vertically suspended operculum; reduced branchiostegals; about 32–35 neural spines; no vertebral centra; a postabdominal bone; long dorsal and anals; median fin rays tending to equal radials; a deep body. In *Gyrodus* and *Bobasatrania* a lateral line branch runs from the skull to the dorsal origin. However the Pycnodontiformes differ in possessing teeth and branchiostegals and in having abdominal pelvic fins (whereas in the Dorypteriformes they are thoracic). In some Pycnodontiformes the supra- and infra-orbital canals join (*Microdon, Eomesodon*), unlike *Bobasatrania*. It therefore seems necessary to regard the Pycnodontiformes as an offshoot of the line which gave rise to the Dorypteriformes and Bobasatraniiformes. This opinion is in agreement with that of Rayner and close to that of Gardiner (1960, 1963). The slender curved branchiostegals, graduating to a point, distinguish the Pycnodontiformes from other orders in Group I.

Three families are included: †Gyrodontidae 1–2/2; †Coccodontidae—no data; †Pycnodontidae 2–5/3.

References. Agassiz (1833–43), Arambourg (1954), Arambourg and Bertin (1958), Berg (1947), Eastman (1914), Gardiner (1960), Rayner (1941), Woodward (1895), Zittel (1887).

†Order PTYCHOLEPIFORMES

Pl. 4

Branchiostegals 10–11; a median gular present; operculum and suboperculum present; ceratohyal and a hypohyal known. Lower Triassic to Lower Jurassic.

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[1] One or two branchiostegals only are reported for the order, and an interhyal, a ceratohyal, and a single hypohyal are now known in *Macromesodon*, Gyrodontidae (*see* fig. 169 by R.J. Nursall *in* J.P. Lehman, 1966. Actinopterygii. Traité de Paleontologie, Tome IV, 3:1–242, 211 fig.).

A single family is included: †Ptycholepidae 10–11/1.
References. Brough (1939), Gardiner (1960), Lehman (1958), Woodward (1895).

†Order **PHOLIDOPLEURIFORMES**

Pl. 5

Branchiostegals 6–14, spathiform; a small median gular and a pair of large lateral gulars are known; operculum and suboperculum present; a ceratohyal and hypohyal known. Lower to Upper Triassic.

A single family is included: †Pholidopleuridae 6–14/3.
References. Lehman (1952), Nielsen (1949), Wade (1935).

†Order **CEPHALOXENIFORMES**

Pl. 5

Branchiostegals and gulars unknown; operculum and suboperculum present. Upper Triassic.

A single family is included: † Cephaloxenidae ?/1.
References. Brough (1939), Lehman (1958).

†Order **AETHODONTIFORMES**

Branchiostegals and lateral gulars unknown; oval median gular present; operculum and suboperculum present. Upper Triassic.

A single family is included: †Aethodontidae ?/1.
References. Brough (1939), Lehman (1958).

†Order **PELTOPLEURIFORMES**

Pl. 5

Branchiostegals 6–7, elongate spathiform; gulars unknown; operculum and suboperculum present. Upper Triassic.

A single family is included: †Peltopleuridae 6–7/1.
References. Brough (1939), Lehman (1958).

†Order **CHONDROSTEIFORMES**

Pls. 5, 6

Branchiostegals about 9–12, spathiform; gulars absent; ceratohyal, perhaps hypohyal—anterior branchiostegal of Watson—and perhaps interhyal present; operculum and suboperculum present. Lower Jurassic.

Discussions under the Acipenseriformes show that Chondrosteidae can be neither closely related nor immediately ancestral to the Acipenseriformes.

From the point of view of the number and form of the branchiostegals, the Chondrosteidae could have developed from the Palaeonisciformes, the Perleidiformes, or the Ptycholepiformes. But the dorsal and anal fin rays equal the basals in the Perleidiformes and Ptycholepiformes and the caudal is symmetrical or nearly symmetrical in Pholidopleuriformes. The latter groups are thus excluded from the ancestry of Chondrosteidae, leaving the Palaeonisciformes. Because of the number of branchiostegals, origin is most likely from the suborder Palaeoniscoidei. This conclusion is in agreement with Watson (1925) who states that "it shows in its skull structure clear evidence of Palaeoniscid origin." Gardiner (1963) suggests that *Chondrosteus* is derivable from the palaeonisciform *Tegeolepis*.

The exact phylogenetic position of the Errolichthyidae is uncertain. The absence of an interoperculum indicates its placement in the chondrostean fishes (Group I). The discussion under Acipenseriformes demonstrates that Errolichthyidae is not closely related nor ancestral to that group. Lehman (1952) is followed in placing the Errolichthyidae in the Chondrosteiformes.

Lehman (1958) isolates the Chondrosteidae in their own order. This separation is affirmed in some measure by the lack of a preoperculum in the Chondrosteidae.

Two families are included: †Chondrosteidae 9–12/1; †Errolichthyidae about 4/1.

References. Hennig (1925), Lehman (1952), Watson (1925), Woodward (1895).

†Order SAURICHTHYIFORMES

Pl. 6

Branchiostegals about 1 (?–3); gulars absent; large semicircular operculum; suboperculum absent. Ceratohyal and hypohyal known. Lower Triassic to Lower Jurassic.

The branchiostegal form in *Saurichthys madagascarensis* is uncertain. The branchiostegal shape in *S. ornatus* is unlike that of any other chondrostean in its extremely elongate form. From the number of branchiostegals it is unlikely that the Saurichthyiformes are related to the Dorypteriformes. Bobasatraniiformes, Redfieldiiformes, or Haplolepiformes. Stensio (1925) indicates that many osteological and sensory canal characters show a close relationship to the Acipenseriformes and concludes that they are intermediate between the Palaeonisciformes and the Acipenseriformes. However, the Saurichthyiformes, lacking a suboperculum, cannot have given rise to the Acipenseriformes which possess one. Further, the supraorbital canal of Saurichthyiformes ends on the frontal whereas in *Acipenser* it joins the infraorbital canal. Thus the Saurichthyiformes cannot be immediately ancestral to the Acipenseriformes, and the long rostrum of the Saurichthyiformes may represent parallelism rather than indicate relationship.

A single family is included: †Saurichthyidae 1(–3 ?)/.[1]

References. Berg (1947), Gardiner (1960), Griffith (1962), Lehman (1952, 1958), Stensio (1925, 1932).

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[1] Obruchev (1964) notes that Belonorhynchidae Woodward 1888 has priority over Saurichthyidae. This being so, the ordinal name should also be changed (Osnovi paleontologii. Beschcliostnie, ribi. Moscow, 522 p.).

Order ACIPENSERIFORMES[1]

Pl. 6

One branchiostegal; operculum deeply engraved or incised; suboperculum present or absent; gulars absent; an interhyal, a ceratohyal, and a hypohyal present. Upper Cretaceous to present. Two families.

Several authors, Traquair (1887), Watson (1925), Aldinger (1937), Stensio (1932), and Lehman (1952, 1958), have forwarded views that the Chondrosteidae are intermediate between the palaeoniscoids and sturgeons or that they were ancestral to sturgeons. Wilimovsky (1956), on the other hand, expressed doubt that the unarmoured Chondrosteidae were ancestral to the armoured Acipenseridae. There are further difficulties in supposing that Chondrosteidae were ancestral. They lack a suboperculum, clavicle, preoperculum, and ribs, all of which are found in Acipenseridae. The caudal is symmetrical in Chondrosteidae, heterocercal in Acipenseriformes. The supraorbital canal, according to Traquair's figures of Chondrosteidae, ends on the parietal but in the Acipenseriformes it joins the infraorbital canal (MacAlpin, 1947). Thus it seems doubtful that the Chondrosteidae were ancestral to the Acipenseriformes. It is possible that they had a common ancestor in the distant past. Gardiner (1963) suggests that the palaeonisciform *Tegeolepis* may have been such an ancestor.

Lehman (1952) described a new fossil fish, *Errolichthys*, which he placed in a separate family in association with Chondrosteidae and Acipenseridae, while he stated (1958) that it was representative of an order having characters in common with the Chondrosteidae and Palaeoniscidae. However, in the Errolichthyidae, as in the Chondrosteidae, the supraorbital canal fails to join the infraorbital canal, and so the Errolichthyidae cannot be close to the Acipenseriformes.

The only chondrosteans in which the infraorbital and supraorbital canals unite are the Redfieldiiformes. The large eyes, short snout, terminal mouth, and developed teeth of the Redfieldiiformes differ from those of the Acipenseriformes. The Phanerorhynchiformes considerably resemble the Acipenseriformes in their long snout, mouth, and rows of scutes but are too specialized in their fins to have been ancestral. However, it is possible that a less specialized ancestor of either the Redfieldiiformes or the Phanerorhynchiformes gave rise to the Acipenseriformes.

Finally, the presence of an operculum and suboperculum argue strongly against Severtzov's association of the Acipenseriformes with the Selachii. These bones are not known in the Selachii; they are found only in the Teleostomi. As ably pointed out in Stensio's (1932) critique of Severtzov, the "selachian" characters of Acipenseriformes, such as the heterocercal tail and spiracle, are primitive characters also shared by generalized Actinopterygii.

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[1] A new Upper Jurassic family, the Peipiasteidae, in which 7 branchiostegals, small opercular, large suboperculum, and a rod-like ceratohyal (flattened and broadened at the extremities) are known, has been described by Liu Hsien-t'ing, Zhou Jia-jian (1965. A new sturgeon from the Upper Jurassic of Lianong, North China. Vert. Palasiatica 9(3): 237–247, 3 fig., 4 pl. (Chinese and English)).

ACIPENSERIDAE

Pl. 6

Branchiostegals. Most authors have stated that branchiostegals are absent. However, examination of a specimen of *Acipenser fulvescens* shows a chevron-shaped bone exposed below the operculum. It is stubby, but definitely a branchiostegal. Dissection reveals a plate of slightly larger extent (which is completely skin-covered in this species) that sends a slight dorsal flange up under the operculum. Holmgren and Stensio (1936) describe and depict the branchiostegal and suboperculum as being at least partly exposed in *Acipenser sturio.* The chevron-shaped branchiostegal of *Acipenser* is reminiscent of the forked branchiostegal found in Polyodontidae. The branchiostegal appears to seat on the interhyal.

Operculars. A large grooved circular operculum with an anterior projection, partly skin-covered, is found. Below it is a small narrow cartilage, the suboperculum. Its dorsal end underlies the operculum. There has been debate whether the large upper bone was an operculum or a suboperculum. But the discovery by Holmgren and Stensio (1936) of a lower gill cover bone, the suboperculum, clearly identifies the large upper element in *Acipenser* as an operculum. Gill membranes joined to isthmus.

Hyoid arch. The hyoid arch is unossified. A short hypohyal, a short ceratohyal round in cross-section, and a cylindrical interhyal are found.

Relationships. The extra-ordinal relationships have already been discussed. Although the families Acipenseridae and Polyodontidae are quite ancient, both reaching back to the Upper Cretaceous period, their branchiostegal apparatuses show considerable similarity. The deeply grooved operculum of *Acipenser* is reminiscent of the incised operculum of *Polyodon* which has degenerated further. The single chevron-shaped branchiostegal of *Acipenser* is not unlike the lone forked branchiostegal of *Polyodon.* The hyoid arches of both contain the same elements and are more or less unossified. *Acipenser* does differ in the possession of a small suboperculum. The ceratohyal of *Polyodon* is longer, a point doubtless related to its longer mandible. Despite the similarities there are many profound differences—scales, rostrum, and so on, which are found in the oldest fossil forms known. Therefore subordinal status may be warranted.

Material examined. Acipenser fulvescens, alizarin specimen, NMC, Ontario.

POLYODONTIDAE

Pl. 6

Branchiostegals. In *Polyodon* there is a single stout branchiostegal which divides distally, after a slight upward bend, into four prongs. MacAlpin (1947) reports three or four branchiostegals in the fossil *Palaeosephurus.* From his photographic plate of the specimen and his drawing it would appear that he may have mistaken the distal divisions of the branchiostegal for separate branchiostegals. It is therefore suggested that *Palaeosephurus* possessed only a single branchiostegal.

Operculars. A much incised large cartilaginous operculum is known in *Polyodon* and *Palaeosephurus.* A suboperculum is absent, but by comparison with

Acipenser the gill cover bone can safely be identified as an operculum. Gill membranes united and free from isthmus.

Hyoid arch. A short hypohyal, a long ceratohyal, and a large quadrate interhyal comprise the hyoid arch. The centre portion of the ceratohyal is ossified.

References. Berg (1947), Gregory (1933), Holly (1936), Holmgren and Stensio (1936), Lehman (1952), MacAlpin (1947).

Material examined. Polyodon spathula, alcoholic specimen, UMMZ, U.S.A.

Group II. HOLOSTEI

With interoperculum (or secondarily lost). Operculars usually entire. Lateral gulars absent. One hypohyal. Lower Triassic to present. Nine orders, two of which are living.

Gardiner (1960) divides his "Holostei" (his quotes) into five superfamilies: Amioidea, Pholidophoroidea, Aspidorhynchoidea, Semionotoidea, and Pycnodontoidea. The last group has here been removed to the Chondrostei, as previously discussed. Gardiner's Semionotoidea contains two families, the Semionotidae (including Berg's Acentrophoridae) and the Lepisosteidae.

Gardiner distinguishes the Semionotoidea on neurocranial characteristics including lack of an orbitosphenoid. It may well be that the semionotoids represent a distinct natural group. If so, they might all be placed in the Lepisosteiformes, amongst the basal Holostei.

Gardiner believes, further, "that the Amioidea and Semionotoidea rose from different Palaeoniscoid stocks." However the presence of an interoperculum, a supramaxillary(ies) (in the semionotids reported at least in *Dapedium*), and a coronoid process, the lack of lateral gulars and clavicles, and the possession of an epihyal and free maxillary are found in both the amioids and semionotoids; these characters are not found in the Chondrostei. To me this suggests that the Amioidea and Semionotoidea share a common ancestor and should be placed in the same supraordinal group, the Holostei.

†Order OSPIIFORMES

Pl. 7

Branchiostegals 9–12, 2 epihyal and 8 ceratohyal, spathiform; one or two median gulars present, primitively with V-shaped pit line; operculum and suboperculum of about equal size; interoperculum present. Interhyal, epihyal, and ceratohyal known. Lower to Upper Triassic.

Lehman (1952) unites the Ospiidae with the Parasemionotidae; Romer (1955) unites the Tungusichthyidae with the Parasemionotidae. Lehman includes *Promecosomina* in the Ospiidae. Stensio (1932) has proposed that the ospiids evolved from the perleids or a perleid-like ancestor; this proposal is in line with the branchiostegal series.

A single family is included: †Ospiidae 9–12/7.

References. Berg (1955), Lehman (1952), Stensio (1932), Wade (1935).

†Order PLATYSIAGIFORMES

Pl. 7

Branchiostegals about 13–20, spathiform; a large gular plate known;

operculum and suboperculum present; interoperculum present. Upper Triassic and Lower Jurassic.

A single family is included: †Platysiagidae 13–20/1.

References. Brough (1939), Gardiner (1960), Lehman (1958).

†Order LUGANOIIFORMES
Pl. 7

Branchiostegals and gulars unknown; operculum and suboperculum present. Upper Triassic.

Brough states that all the characters are holostean except *a*) the absence of an interoperculum and the gill cover with almost equal operculum and suboperculum, *b*) the plate-like preoperculum. But the portion of the head which would contain the interoperculum (and branchiostegals) appears to be missing. The preoperculum, although plate-like, broadens ventrally interposing itself between the jaws and operculars in a distinctly holostean manner. The operculars and suboperculars are not unholostean. On the positive side they have firm holostean features such as a free maxillary and a coronoid process. They are therefore provisionally placed amongst the Holostei.

A single family is included: †Luganoiidae—no data/1.

References. Brough (1939), Lehman (1958).

Order AMIIFORMES (SEMIONOTIFORMES)
Pls. 7, 9

Branchiostegals 5 or 6–30; 0–4 epihyal and 10–21 ceratohyal; median gular present, with or without V-shaped pit line; operculum, suboperculum, and interoperculum present; interhyal, epihyal, ceratohyal, and one hypohyal present. Upper Permian to present.

It seems likely that the Amiiformes share a common ancestry with the Ospiiformes (Brough, 1939; Gardiner, 1960).

Ten families, one of which is living, are included: †Furidae (Caturidae, Eugnathidae) 6–25/8; †Acentrophoridae 9–10/1; †Paracentrophoridae 10/1; †Semionotidae 3–14/4; †Catervariolidae 6/1; †Signeuxellidae +1/1; †Macrosemiidae 5–10/3; †Sinamiidae ca.14/1; †Lombardinidae unknown/1; Amiidae 10–13/2.

References. Agassiz (1833–43), Arambourg and Bertin (1958), Berg (1947, 1955), Brough (1939), Eastman (1914), Gardiner (1960, 1963), Gill (1923), Gregory (1923), Hubbs (1920), Jordan and Evermann (1896), Lehman (1949), Rayner (1941), Romer (1955), Saint-Seine (1955), Schaeffer (1960), White and Moy-Thomas (1940), Woodward (1895, 1902–1912), Zittel (1887).

AMIIDAE
Pl. 9

Branchiostegals. Amia 10–13; †*Megalurus* 11–12. Form elongate and spathiform with curved tips. The branchiostegals all insert on the ceratohyal. The uppermost branchiostegal is dilated and has been termed the branchioperculum by Hubbs.

Gular. A large median gular is present in *Amia.* Its length is about two-thirds that of the mandibles.

Operculars. Operculum larger than the suboperculum and sending a wedge down into it. Interoperculum small, elongate, and triangular.

Hyoid arch. A triangular hypohyal, angulate large ceratohyal, triangular epihyal with a prong inserting on outer ceratohyal, and small cylindrical unossified interhyal.

Material examined. Amia calva, 11 alizarin specimens, NMC58-192-S, Pt. Pelee, Ontario; 12 alizarin specimens, NMC58-209, Georgian Bay, Ontario; alcoholic specimen, BC59-426, Illinois.

References. Agassiz (1833–43), Berg (1947), Hubbs (1920), Jordan and Evermann (1896).

Order LEPISOSTEIFORMES (LEPIDOSTEIFORMES)

Pls. 8, 9

Branchiostegals 3, spathiform; gulars absent; operculum and suboperculum present; interoperculum absent; epihyal, ceratohyal, and hypohyal present. Upper Cretaceous to present. A single family.

The generic name was originally spelled *Lepisosteus* by Lacépède. This spelling has been incorrectly amended to *Lepidosteus* by some authors.

Arambourg and Bertin (1958) include the Lepisosteidae in the same order as *Amia.* The many skeletal oddities of Lepisosteidae would, in my opinion, justify its ordinal separation.

The modifications of the skull of Lepisosteiformes make its placement difficult. Most authors include it in Holostei. The non-platelike form of the preoperculum, the rudimentary clavicle, the absence of a cosmine layer in the scales, the maxillary not being immovably connected with the preoperculum, dorsal and anal pterygiophores each supporting a single ray, and the tail not being heterocercal are characters indicating holostean placement. However, the fin rays are completely segmented, and some of the above holostean characters might be modifications resulting from the peculiar jaws. Thus the question of placement is not entirely settled. Rayner (1948), from neurocranial study, believes that the Lepisosteidae are derivable from the Semionotidae. Gardiner (1960) also considers such an origin to be likely.

LEPISOSTEIDAE

Pls. 8, 9

Branchiostegals. 3 small spathiform branchiostegals. The upper two are attached to the epihyal, the other to the ceratohyal. The uppermost branchiostegal is broad; the lower two are attenuate.

Gulars. Absent.

Operculars. An operculum and suboperculum of approximately equal size are present; the first sends a wedge into the latter.

The absence of an interoperculum in this presumably holostean fish has caused a number of authors to identify other elements as the interoperculum. The preoperculum has been identified as an interoperculum by Regan (1923). The passage of the preoperculo-mandibular canal through this bone clearly identifies it as the preoperculum, however. Holmgren and Stensio (1936) call the small bone above the anterior end of the preoperculum the interoperculum. However, this bone develops there; it lies above the preoperculo-mandibular canal and is far from the epihyal and suboperculum which interopercula normally contact. This bone is therefore probably the quadrato-jugal, as suggested by Hammarberg (*in* Arambourg and Bertin, 1958). The upper branchiostegal has also been identified as the interoperculum (de Beer, 1937). But this element does not lie in the same horizontal fold as the suboperculum, does not lie over the outer face of the epihyal, and does not insert on the suboperculum or jaw; these relationships make it difficult to identify it as an interoperculum. It must therefore be considered that the interoperculum was lost (or perhaps was never present, in which case Lepisosteiformes should be placed in the Chondrostei). The very anterior jaws and the downward expansion of the preoperculum into the normal position of the interoperculum are both changes which could have led to the loss of the interoperculum.

Hyoid arch. Consists of a hypohyal, a short ceratohyal round in cross-section, and a short epihyal with a small backward projection on which sits the upper branchiostegal. A small cartilage on top of the epihyal may represent the interhyal.

References. Arambourg and Bertin (1958), de Beer (1937), Berg (1947), Boulenger (1904), Regan (1923).

Material examined. Lepisosteus osseus, alizarin specimen, NMC60-478-A, Ontario; skeletal specimen, USNM 110191, U.S.A.

†Order **ASPIDORHYNCHIFORMES**

Pl. 8

Branchiostegals 12–13, spathiform; gulars absent; large operculum and small suboperculum present; advanced interoperculum present. Middle Jurassic to Upper Cretaceous.

A single family is included: †Aspidorhynchidae 12–13/1.

References. Agassiz (1833–43), Assman (1906, *in* Berg, 1947), Gardiner (1960, 1963), Woodward (1895).

†Order **PACHYCORMIFORMES**

Pl. 8

Branchiostegals (6+) 30–50, with about 22 epihyal and 20 ceratohyal, spathiform; median gular present; lateral gulars apparently absent; equal-sized operculum and suboperculum; triangular fairly advanced interoperculum present; epihyal, ceratohyal, and hypohyal present. Upper Triassic to Upper Cretaceous.

Following Romer (1955) and Arambourg and Bertin (1958), Protosphyraenidae is synonymized with Pachycormidae. Woodward (1895) said that *Protosphyraenus* differed little from *Hypsocormus* (Pachycormidae). However, contrary to Arambourg and Bertin, the Pachycormidae is not placed in the same order as the Amiidae. In addition to the characters by which Berg distinguished the Pachycormiformes, there are the greatly enlarged lower postorbital and the numerous branchiostegals.

A single family is included: †Pachycormidae 6 (+?), 30–50/2.

References. Lehman (1949), Woodward (1895, 1898), Zittel (1887).

†Order PHOLIDOPHORIFORMES
Pl. 8

Branchiostegals 1 (?) 5+–18+, spathiform; narrow or large gular plate; operculum, suboperculum, and interoperculum present; epihyal, ceratohyal,[1] and probably interhyal present. Middle Triassic to Upper Cretaceous.

Eight families are included: †Ichthyokentemidae about 5–7/1; †Pholidophoridae 7–17†/1; †Pleuropholidae †2/1; †Liguellidae †1/1; †Majokiidae not preserved/1; †Oligopleuridae 6–13/2; †Galkiniidae 10/1[2]; †Archaeomaenidae about 8/1.

References. Berg (1947), Bertin and Arambourg (1958), Griffith and Patterson (1963), Rayner (1948), Saint-Seine (1955), Woodward (1890, 1895, 1895*a*).

†Order LEPTOLEPIFORMES
Pl. 8

Branchiostegals about 21 with 9 epihyal and 12 ceratohyal. Median gular present. Operculars complete and entire. Interhyal, epihyal, perforated ceratohyal, and one hypohyal present. Middle Triassic to Middle Cretaceous (Griffith and Patterson, 1963).

The distinctive combination of characters warrants the ordinal recognition accorded by Tretiakov (1945) and by Arambourg and Bertin (1958).

Woodward, Regan, Berg, and Romer include the Leptolepidae amongst the teleostean fishes. The principal basis for the placement of Leptolepidae among the teleosteans rather than among the holosteans is their possession of intermuscular bones, unknown in (other) holosteans. However, in opposition to this the Leptolepidae possess a coating of ganoin on their scales and external bones, a feature unknown in the teleosteans. Two other characters turn the balance in favour of holostean placement: the sensory canals on the head of Leptolepidae are more primitive than in the teleosts (Rayner, 1937); and there is only a single hypohyal, whereas all the clupeiforms (except Phractolaemidae) have two. The Leptolepidae may therefore be best placed in the Holostei as the terminal order that gave rise to the teleosts. Chronologically this placement is more satisfactory. The Leptolepidae are known from the Middle Triassic or at least the Jurassic. None of the Clupeiformes are known previous to the Upper Jurassic. Arambourg and Bertin (1958) also consider the Leptolepidae to be subteleostean, but they place them in a different supraordinal category, the Halecostomi, along with the Pholidophoriformes and Aspidorhynchiformes.

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[1] The ceratohyal is imperforate in *Pholidophorus bechei* (O. Nybelin, 1966. On certain Triassic and Liassic representatives of the family Pholidophoridae. S. Str. Bull. British Mus. (Nat. Hist.), Geol. 11 (8): 351–432, 15 pl., 16 text-fig.).

[2] Obruchev, E. I. 1964. Osnovi paleontologii. Bescheliostnie, ribi. Moscow, 522 p.

A single family is included: †Leptolepidae about 21/1[1].

References. Berg (1947, 1948), Gardiner (1960), Nybelin (1963), Rayner (1937), Tretiakov (1945), Woodward (1895).

Group III. TELEOSTEI

With interoperculum (or secondarily lost). Operculars entire or with spines. Lateral gulars absent. Two hypohyals (or secondarily one or both lost). Thirty-four orders.

Malacopterygii

Branchiostegals 0–36, often one or more spathiform, sometimes filiform, virgaform, or acinaciform. Median gular only in primitive clupeiforms. Epihyal and ceratohyal separate (except Siluroidei). Never spines on opercular bones. Seldom with an acanthopterygian pattern of 4 external and none or some ventral or internal (4+X). Seven orders.

The division of teleost fishes into malacopterygian and acanthopterygian on the basis of branchiostegals has recently received valuable support in a study on the retractores arcuum branchialium by Holstvoogd (1963). Holstvoogd (1963 and *in litt.*)[2] reports that the malacopterygian groups studied—Clupeiformes, Mormyriformes, Cypriniformes, Notacanthiformes, Anguilliformes (and Polypteriformes)—lack the muscle retractores arcuum branchialium. On the other hand, the acanthopterygian groups studied—Gadiformes, Gasterosteiformes, Syngnathiformes, Beryciformes, Ophidiiformes, Percopsiformes, Atheriniformes, Perciformes, Pleuronectiformes, Gobiesociformes, Tetraodontiformes, Echeneiformes, Mastacembeliformes, and Batrachoidiformes—possess this muscle. The Myctophiformes also possess this muscle; as is discussed later they are here placed amongst the acanthopterygians. Conclusions from this pharyngeal study and the study of branchiostegals are in very close agreement.

The Malacopterygii, as here understood, may be characterized as follows: branchiostegals spathiform (at least the uppermost), virgaform, or filiform and seldom arranged in the 4 external + X ventral or internal pattern[3]; gape of the upper jaw bordered by both premaxillary and maxillary; without retractores arcuum branchialium muscle; pelvics abdominal or subabdominal; and inner pelvic ray not fused to radial; scales cycloid; gas bladder, physostomus, if present; may possess a mesopterygoid arch; epihyal not sutured to ceratohyal; operculars, preoperculum, and suborbitals spineless; premaxillaries non-protractile; without true fin spines. The adverb 'usually' may be appended to most of the above characterizations. Seldom do superordinal characteristics apply to all the thousands of included species. (This fact does not negate the taxon—they are not key characters—since the similarities are parallelisms.) In contradistinction to the Malacopterygii *see* the characterization of the Acanthopterygii, p. 89.

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[1] †Protelopidae is provisionally placed in the Leptolepiformes. Although Saint-Seine included it in the Elopoidei, its perforated ceratohyal, single hypohyal, cephalic pit line pattern, and pelvic structure would favour holostean placement, despite its lacking a parasphenoid process (Saint-Seine, P. 1949. Les poissons des calcaires lithographiques de Cerin. Nouvelles Archives Mus. d'Hist. Nat. Lyon., Fasc. 2: 1–351, 26 pl., 120 text-fig.).

[2] This excellent study has now been published in full. C. Holstvoogd. 1965. The pharyngeal bones and muscles in Teleostei, a taxonomic study. Proc. Koninkl. Nederl. Akademie van Wetenschappen, Amsterdam, Ser. 3, 68 (3): 209–218, figs. 1–13, photos 1–5.

[3] The pattern is variable in Malacopterygii, rarely being 4 + X, but in the Acanthopterygii it is highly constant, almost always being 4 + X. X may equal 0–17 branchiostegals.

Order **CLUPEIFORMES (ESOCIFORMES[1], GALAXIIFORMES, GONORHYNCHIFORMES[1], CHANOIFORMES[1])**

Pls. 9, 10

Branchiostegals 1–36 with 0–1 interhyal, ½–12 epihyal, 0–23 ceratohyal, and 0–5 hypohyal, with 2–12 external and 0–11 ventral (or rarely internal), spathiform. Median gular present only in Albuloidei and more primitive suborders. Operculars complete, usually entire (rarely crenulate). Interhyal, epihyal, ceratohyal, and two hypohyals present (except no interhyal in chanoids and only one hypohyal in Phractolaemidae[2]). Gill membranes separate, rarely united and free from, or joined to the isthmus. Fifty-six families, twelve of which are known only from fossils. Upper Jurassic to present (Nikolsky (1954) reports formations with *Lycoptera* as not Lower Cretaceous but Upper Jurassic).

Gosline (1960) divided the Clupeiformes into two divisions, Clupei and Osteoglossi. The Osteoglossi, with the exception of Hiodontidae, are here removed to the Mormyriformes, as discussed under that order. The Hiodontidae are placed in a new suborder within the Clupeiformes.

Although the Clupeiformes do show some relationship to the Pachycormiformes, there seems little doubt that their closest relationships are to the Pholidophoriformes and Leptolepiformes. The Leptolepiformes are closer to the Clupeiformes in having intermuscular bones which are absent in the Pholidophoriformes.[3] Primitive Clupeiformes and Pholidophoriformes have bone cells in their scales, but Leptolepiformes lack them. On the latter basis Gardiner (1963) suggests that the Pholidophoriformes and not the Leptolepiformes are ancestral to the Clupeiformes.

Some authors have considered that Elopoidei may belong in the Holostei (Saint-Seine, 1956; Nybelin, 1957) on the basis of such characters as the ethmoid commissure connecting the infraorbital canals and the possession of a gular. However, these characters may be regarded as primitive holdovers. The developments of a second hypohyal and of a modern scale type clearly distinguish the members of the Clupeiformes from their predecessors. The only alternative solution would be placement of the Lycopteroidei and Elopoidei together in their own order. But this has little merit since the Albuloidei still retain a vestige of a median gular. It is preferable not to establish an order on the basis of a slowly receding character.

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[1] Mednikov, B.M. 1962. Bull. Moscow Soc. Nat. 67: 155–156.

[2] And Cromeriidae.

[3] But intermuscular bones are now in the Pholidophoriformes (Lund, Richard 1966. Intermuscular bones in *Pholidophorus bechei* from the Lower Lias of England. Science 152 (3720): 348–349, illus.). This further weakens the use of this character for separating the Holostei and Teleostei and strengthens the case for placement of the Leptolepiformes in the Holostei, as suggested here.

Gardiner (1960, fig. 79) suggests that the clupeiforms are diphyletic. However, they are united by the possession of two hypohyals in contrast to the preceding orders. It thus seems more likely that they had a common origin.

†Suborder **Lycopteroidei**

†LYCOPTERIDAE

Branchiostegals. At least 6 or 8 to 10, spathiform. *Lycoptera middendorffi* 10, with 3 epihyal and 7 ceratohyal.
Gular. A median gular present in *Lycoptera*, less than one-half length of mandible.
Hyoid arch. Epihyal, ceratohyal, and two hypohyals known.
References. Berg (1948*a*, 1955), Woodward (1895).

Suborder **Elopoidei**

Branchiostegals +15–36 with 5–13 epihyal and 10–23 ceratohyal, about 12 being ventro-lateral and 20–23 being ventral, the upper ones spathiform and the lower ones becoming slender. A well-developed but narrow median gular one-third to three-quarters the length of the mandible. Two hypohyals. Operculars complete and entire. Gill membrane separate. Five families, two living.

Jordan, Evermann, and Clark (1930) include the elopid and albulid families in separate suborders. Berg (1947) places both in the Suborder Clupeoidei. Gosline (1960) places both in the Suborder Elopoidei (separate from the Clupeoidei) but recognizes two superfamilies, Elopoidae and Albuloidae. It is my opinion that Jordan, Evermann, and Clark were correct in awarding subordinal status to the two groups. The two groups differ in numerous profound characters and are more trenchantly separated than many other well-recognized suborders. The Albuloidei (Albulidae and Pterothrissidae) differ trenchantly from the Elopoidei (Elopidae and Megalopidae) in the following characters: 1–3 branchiostegals instead of 5–13 on the epihyal; gular plate vestigial or absent versus well-developed; one versus two supramaxillaries; pelvic rays 10–14 instead of 15–17; maxillaries toothless instead of toothed; ventral instead of terminal or superior mouth; gill rakers tubercle-like instead of long and slender; only 2 pairs of uroneurals instead of 4 pairs; terminal vertebra with no neural arch and with a greatly expanded median crest behind it, instead of with a neural arch and a small median crest; 7 hypurals instead of 8–9; one postterminal centrum instead of two (characters from Berg, 1947; Hollister, 1939; Gosline, 1961; Gregory, 1933). These differences show that the albuloids are considerably advanced with respect to the elopoids. Ridewood (1904) came to a similar opinion after study of their skulls: "There is no doubt that the Elopidae are the most archaic of existing teleosteans and that the Albulidae are in few respects more highly specialized; but the study of the skull does not show any direct affinity between the two families." Nybelin (1960), although he discovered the rudimentary gular plate in *Albula*, felt that "The detection of this plate naturally does not mean that *Albula vulpes* would have a closer relationship to the Elopidae and Megalopidae than what has so far been assumed, for it is clear from other facts *Elops*, *Megalops* and *Albula* all represent evolutionary lineages of their own." The two groups are therefore treated as separate suborders.

ELOPIDAE (†RAPHIOSAURIDAE)

Branchiostegals. Vary from 15 or more to 36, but 27–35 in living members: †*Laminospondylus transversus* 16 or more; †*Rhacolepis* about 20; †*Thrissopater* about 30; †*Esocelops* at least 15; †*Spaniodon* at least 15; †*Osmeroides* 20 with 5 broad ones on the epihyal and 15 on the ceratohyal; †*Pachyrhizodus* 9–10 on the epihyal; *Elops* 24–36 with 12 epihyal and 20–23 ceratohyal: the upper 12 are slightly on the lateral face and the remainder are on the ventral face of the arch, the upper ones being broad and expanded, the lower narrow and elongate.
Gular. In *Elops* elongate narrow median gular occupying about one-third the length of the mandibles; no pit line apparent on it. In *Esocelops* gular at least three-quarters the length of mandible. In *Osmeroides* long and narrow, its length slightly more than half the mandible length.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Elops*.
References. Fowler (1936), Regan (1909), Ridewood (1904), Springer (1957), Weber and de Beaufort (1913), Woodward (1901, 1902–1912).
Material examined. Elops saurus, five alcoholic specimens, BC55-321, Louisiana; skeleton, USNM 26218, Key West.

MEGALOPIDAE

Branchiostegals. Megalops 23–27 with 13 epihyal and 10–12 ceratohyal. The ranges of counts in the two species *atlanticus* and *cyprinoides* are identical.
Gular. A narrow elongate diamond-shaped gular without trace of pit line. Its length slightly exceeds half the length of the mandible.
Hyoid arch. An interhyal, epihyal, ceratohyal, and two hypohyals present.
References. Day (1875), Fowler (1936), Ridewood (1904), Weber and de Beaufort (1913).
Material examined. Megalops atlanticus, one skeleton, USNM 179715, Guyana.

†GANOLYTIDAE

Branchiostegals. No data available.

Suborder **Albuloidei**

Branchiostegals (4) 6–16 with 2–3 epihyal and 10–12 ceratohyal, 11 external and one ventral. A rudimentary gular present or absent. Operculars complete and entire. Gill membranes separate. Interhyal, epihyal, ceratohyal, and two hypohyals present. Two families.

ALBULIDAE
Pl. 9

Branchiostegals. †*Chanoides* probably about 4; †*Ancylostylos* probably 6; *Albula* 10–16. *Albula vulpes* observed (10) 11–13 left and 10–11 right with 2 epihyal and 10 ceratohyal, 11 external and 1 ventral.

Whereas (10) 11–13 branchiostegals were found in 14 specimens from the Pacific coast of America (Peru to Mexico), Day (1875), Misra (1953), and Weber and de Beaufort (1913) report 14–16 from India and the Indo-Australian Archipelago. This might suggest that two species are involved. In *Albula vulpes* the upper branchiostegals are broadly spathiform becoming narrower ventrally; they are all decurved and have a median external ridge basally. The lowest ones may not contact the ceratohyal but may be free in the membrane.

Gular. Nybelin (1960) discovered the presence of a very slender median gular about half the length of the mandible in *Albula vulpes.* It is rudimentary compared to that of the elopoids. In 3- and 6-inch specimens only a threadlike trace was observed. The gular is contained in a gular fold which, curving anteriorly, joins the two mandibles. The posterior border of the fold is crenulate.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals.

References. Misra (1953), Ridewood (1904), Weber and de Beaufort (1913), Woodward (1901).

Material examined. Ten specimens of *Albula vulpes,* BC56-160, Peru, one of which was cleared and stained for detailed examination; three alcoholic specimens, BC59-687, Panama, Panama; one alcoholic specimen BC56-162, Talara, Peru; one alcoholic specimen, BC60-14, Acapulco, Mexico.

PTEROTHRISSIDAE

Branchiostegals. †*Istieus* about 10; *Pterothrissa gissu* 6.

Gular. Pterothrissa lacks a median gular plate.

References. Günther (1887), Tomiyama and Abe (1958), Woodward (1901).

Material examined. None.

Suborder **Clupeoidei**

Branchiostegals 5–20 with 1–5 epihyal and 0–11 ceratohyal, 2–10 external and 0–11 ventral. Gular absent. Operculars complete and entire (except that they may be crenulate in alepocephalids). Gill membranes separate. Interhyal, epihyal, ceratohyal, and two hypohyals in all families examined. Three superfamilies, fourteen families, four of which are known only from fossils.

The branchiostegal rays of Alepocephaloidea tend to be long and slender whereas at least the upper branchiostegals of Clupeoidea and Chirocentroidea are broad and one or more bears a clupeoid projection. The branchiostegals of Rosauridae are suggestive of the Alepocephaloidea. For classification of the Clupeoidei *see* Whitehead (1963). He, however, omits the alepocephaloids from the suborders, but they are retained provisionally in the clupeoids here until their true status and position is definite.[1] Probably they do deserve subordinal recognition.

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[1] Gosline (1965, Copeia (2): 186–194) also excludes the alepocephaloids. To his characterization of the Clupeoidei (*sensu stricto*) may be added the presence of the clupeoid projection on the branchiostegal(s).

Judging by the presence of the maxillary in the gape and other features, the acanthopterygian pattern of 4 + X in Alepocephalidae is only a chance resemblance, not one denoting relationship.

Superfamily ALEPOCEPHALOIDEA

ALEPOCEPHALIDAE

Branchiostegals. Vary from 5–9, but 13 in *Leptochilichthys*, all slender and lath- or rod-shaped. *Alepocephalus* 6, *Anamalopterichthys* 7, *Asquamiceps* 5, *Aleposomus* 6–7, *Bathytroctes* 1–8, *Bellocia* 6, *Conocara* 6, *Ericara* 6, *Grimatotroctes* 7, *Leptoderma* 7, *Leptochilichthys* 13, *Macromastax* 9, *Micrognathus* 7, *Mitchillina* 6, *Narcetes* 8, *Nemabathytroctes* 7, *Photostylus* 6, *Rouleina* 6, *Talismania* 6–8, *Tauredophidium* 8, and *Xenodermichthys* 6–7. *Talismania bifurcata* 7 with 4 epihyal and 3 ceratohyal, 4 external and 3 ventral, slender elongate, and distally slightly laminar.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Talismania.*

Relationships. Leptochilichthys differs quite strongly from other alepocephaloids in having 13 branchiostegals instead of 5–9.

References. Beebe (1933), Fowler (1936), Garman (1899), Grey (1958), Günther (1887), Maul (1948), Misra (1953), Parr (1937, 1951, 1952), Tucker (1954), Weber and de Beaufort (1913).

Material examined. Bathytroctes rostratus, alcoholic specimen, USNM 137754-9, Philippines; *Talismania bifurcata,* alcoholic specimen, BC62-159, California.

SEARSIIDAE

Branchiostegals. Vary from 4 to 8. *Persparsia* 7, *Pellisolus* 7, *Holtbyrnia* 7–8, *Searsia* 7–8, *Normichthys* 8, *Mirorictus* 4, *Platytroctes* 5–6, *Sagamichthys* 6, *Maulisia* 7–8, *Mentodus* 7–8, *Barbantus* 7–8. *Xenodermichthys copei* 6 with 3 external epihyal and 3 ventral ceratohyals, upper acinaciform, lower virgaform.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals.

Material examined. Xenodermichthys copei, alcoholic specimen, NMC64-434, Bay of Biscay, France.

Relationships. Parr (1951) separated this family from Alepocephalidae. It is very closely related to the Alepocephalidae, being distinguished only by the presence of the shoulder organ. The similarity of the branchiostegal counts would confirm the closeness of the relationship.

References. Maul (1954, 1957), Parr (1951, 1960), Tucker (1954).

MACRISTIIDAE (*See* Note 2, Addenda.)

Branchiostegals. Long, slender, curved, with about 8–10 in *Macristium.*

Relationships. Regan first placed this fish in the family Scopelidae; later he modified his view making it a distinct family close to the Alepocephalidae. Berg followed the latter view but stated that its position was uncertain. Marshall (1961), after the capture of a second young specimen, suggested that *Macristium* was the survivor of the fossil ctenothrissid fishes.

I am inclined to disagree with the latter opinion in concurrence with Patterson (1964). Although the number of branchiostegals in the Ctenothrissidae and Macristiidae is about the same, the form of the branchiostegals is not: the upper two branchiostegals in Ctenothrissidae are broad and spathiform whereas in Macristiidae all the branchiostegals are narrow. Scales are absent in Macristiidae, present in Ctenothrissidae. As Marshall points out, the Macristiidae lack supramaxillaries whereas there are two well-developed ones in the Ctenothrissidae. The number of vertebrae differs by about twenty. The similarities in fin pattern and mouth angle may be a result of similarity in habits; they are not strong subordinal characteristics. On the other hand, the Macristiidae are similar to the Alepocephalidae in many of the listed characters, such as the structure of the upper jaw and teeth, the slender branchiostegals, and the absence of scales. In some Alepocephalidae the ventrals are almost thoracic and the dorsal is central in position, thus approaching the Macristiidae.

References. Marshall (1961), Regan (1911*d*).

Material examined. None.

Superfamily CHIROCENTROIDEA

†ICHTHYODECTIDAE

Branchiostegals. No information available.

Relationships. According to Woodward (1901) the vertebral axis, fins, and scales are similar to those of *Chirocentrites.*

CHIROCENTRIDAE[1]

Branchiostegals. Vary from 6–8 to 20. *Chirocentrus* 6–8 with 2–3 on the epihyal and 4–5 on the ceratohyal; the ones on the epihyal are on the external, those on the ceratohyal on the ventral face of the arch; the upper 2–3 spathiform, the lower scythe-shaped. *C. hypsoseloma* 6 and *C. dorab* 8. The uppermost with a clupeoid projection. †*Platinx* 6–7, †*Chirocentrites* about 20.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals; ventral side of ceratohyal notched for reception of branchiostegals.

Relationships. The Chirocentridae differ from the Alepocephalidae and Searsiidae by the breadth of the upper branchiostegals which are narrow in the other two families. The fossil *Chirocentrites* with 20 branchiostegals differs trenchantly from *Chirocentrus* with only 6–8. It might be suggested that *Chirocentrites* does not belong in this family. Bertin and Arambourg (1958) have placed *Chirocentrites* in the family †Ichthyodectidae. This placement cannot be evaluated from the point of view of branchiostegals since branchiostegals are unknown in the Ichthyodectidae. Berg (1940) places the Icthyodectidae and Chirocentridae together in the suborder Chirocentroidei. Whitehead (1963*b*) places the Chirocentridae in its own superfamily amongst the Clupeoidei. The latter path is followed here (*see* fn. p. 39).

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[1] A valuable paper on these fishes has been published by D. Bardack (1965, Anatomy and evolution of chirocentrid fishes. U. Kansas Paleontol. Contrib., Vertebrata (10): 1–88, 2 pl., 27 text-fig.). According to Bardack, *Platinx* may not belong in the family and the Chirocentridae are derived from the pholidophorids. The possession of basipterygoid processes on the parasphenoid by fossil chirocentrids would certainly suggest holostean ancestry. But the living *Chirocentris* lacks these and shares eight other characters with the clupeoids (p. 31), which Bardack ascribes to parallelism. It seems to me unlikely that so many characters would be parallel through chance, and rather that they indicate relationship to the clupeoids. *Chirocentris* has, as shown above, 2 hypohyals indicating teleostean rather than holostean placement. If these suggestions are right, *Chirocentris* would be placed near or amongst the clupeoids, and the remaining genera, all fossil and pre-Tertiary, would be placed amongst the advanced Holostei.

References. Chevey (1932), Day (1875), Ridewood (1904*a*), Woodward (1901).

Material examined. Chirocentrus hypsoseloma, alcoholic specimen, BC58-32, Malaya; *Chirocentrus dorab*, alcoholic specimen, USNM 47990, Cochin. China.

Superfamily CLUPEOIDEA

DUSSUMIERIIDAE

Pl. 9

Branchiostegals. Vary from 6 to 20. *Ehirava, Sauvagella, Spratelloides*, and *Jenkinsia* 6. *Gilchristella* 6–7 with 2 epihyal and 4 ceratohyal, 4 external and 2 ventral; branchiostegals spathiform with clupeoid projections. *Dussumieria* 12–20 with 3½–5 on the epihyal and 8–8½ on the ceratohyal, all on the external surface. *Etrumeus* 13–15 bearing 4 on the epihyal and 9–10 on the ceratohyal, all on the external surface. †*Histiothrissa* 15. In *Etrumeus* most of the upper branchiostegals are broad and spathiform and bear an anterior projection at the base.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Etrumeus, Dussumieria*, and *Gilchristella*. In *Dussumieria* the epihyal possesses a foramen, and it and the ceratohyal emit small prongs toward one another on their internal faces.

Relationships. The number of branchiostegal rays indicates the Dussumierinae to be more primitive than the Spratelloidinae. *See* Whitehead (1936*b*) for an excellent revision of this family and discussion of its relationships.

References. Chapman (1948*a*), Misra (1953), Munro (1955), Ridewood (1904*a*), Schultz *et al.* (1953), Weber and de Beaufort (1913), Whitehead (1962, 1963*b*).

Material examined. Alizarin specimens of *Gilchristella aesturarius*, NMC62-141, South Africa; *Dussumieria acuta*, alizarin specimen, NMC63-71-S, Singapore; *Etrumeus teres*, alizarin specimen, NMC63-70-S, Nagasaki, Japan.

ENGRAULIDIDAE

Branchiostegals. Vary from 7–19 with 1–3 epihyal, 8½–11 ceratohyal, and 4–10 external and 0–11 ventral. *Anchoviella* 11–13, *Setipinna* 11–19, *Thrissocles* 10–14, *Scutengraulis* 12–14, *Anchoa* 10–15, *Coilia* 7–13, *Stolephorus* 11–13, *Engraulis* 9–14, *Lycothrissa* 7–12. *Anchoa compressa* 10 with 1 epihyal and 9 ceratohyal, 10 external and 1 ventral, the uppermost broad and spathiform, the lower becoming narrower, all with a clupeoid projection. *Engraulis encrasicholus* 10 with 1 epihyal and 9 ceratohyal. *Coilia nasus* 11 with 2½ epihyal and 8½ ceratohyal. *Anchoa hepsetus* 15 with 3 epihyal, 11 ceratohyal, and 1 hypohyal, 4 external and 11 ventral, the upper ones broad and spathiform, all with a clupeoid projection on the base.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Anchoa*, *Engraulis*, and *Coilia*.

Relationships. The form of the branchiostegals indicates that the Engraulididae are related to the Dussumieriidae.

References. Chapman (1944), Chevey (1932), Day (1875), Inger and Kong (1962), Misra (1953), Ridewood (1904*a*), Smitt (1895), Weber and de Beaufort (1913).

Material examined. Anchoa hepsetus, alizarin specimen, NMC62-73, North Carolina.

†CLUPAVIDAE

Branchiostegals. Figure 1,584 of Bertin and Arambourg (1958) shows that *Clupavus* bears at least 4 spathiform branchiostegals.

Relationships. According to Bertin and Arambourg the Clupavidae may be placed in the neighbourhood of the Dussumieriidae.

Reference. Bertin and Arambourg (1958).

†PSEUDOBERYCIDAE

Branchiostegals. No information available.

Relationships. Allied to the Clupeidae according to Berg. The scales are pectinate.

References. Berg (1947), Woodward (1901).

†SYLLAEMIDAE

Branchiostegals. In †*Syllaemus* there are 10 delicate branchiostegal rays on the ceratohyal.

Relationships. According to Berg the Syllaemidae are allied to the Clupeidae.

References. Berg (1947), Woodward (1902–1912).

DOROSOMATIDAE

Pl. 9

Branchiostegals. Vary from 5–6. *Dorosoma* 5–6 with 1 epihyal and 4 ceratohyal, 3 external and 2 on the ventral face of the hyoid arch; the upper three branchiostegals are broad and scimitar-like, the lower two acinaciform. The upper three have clupeoid projections at the base. *Nematalosa* 6 with 1½ epihyal and 4½ ceratohyal.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals.

Relationships. Relationship to the Clupeidae, Engraulididae, and Dussumieriidae is clearly shown by the possession of a clupeoid projection at the base of the upper branchiostegals.

References. Day (1875), Ridewood (1904*a*), Vladykov (1945).

Material examined. Dorosoma cepedianum, alizarin specimens, NMC60-521-A, Lake St. Claire, Canada.

CLUPEIDAE

Pl. 10

Branchiostegals. Vary from 6 to 10 with 1½–3 epihyal and 4–8 ceratohyal, 3 external and 4–7 ventral. *Alosa* 7; *Sardinops* 7 with 1½ epihyal and 5½ ceratohyal; *Opisthonema* 6 with 2 epihyal and 4 ceratohyal; *Clupea harengus pallasii* 8–9 with 2 epihyal, 7–8 ceratohyal, 3 external and 6–7 ventral; *Adontostoma*, *Sardinella*, *Ilisha*, *Corica*, *Clupeoides*, *Cynothrissa*, *Amblygaster*, *Pellona*, *Limnothrissa*, *Odaxothrissa*, *Opisthropterus*, and *Raconda* 6; *Herklotsichthys* 5–6; †*Scombroclupea*, †*Diplomystus* about 10; *Stolothrissa* 6–7; *Potamothrissa* 5–7; *Microthrissa* 5; *Poecilothrissa* 5–6; *Alosa pseudoharengus* 7 with 2 epihyal and 5 ceratohyal, 3 being external and 4 being ventral, the ventral ones being inserted in notches. *Opisthopterus dovi* 6 with 2 epihyal and 4 ceratohyal, 3 external and 3 ventral. In these genera the upper three branchiostegals are usually wide and spathiform, and the lower ones are slender. An anterior projection arises from the base of at least the upper branchiostegals. †*Scombroclupea*, according to Woodward's figure, does not bear these projections.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Clupea*, *Opisthopterus*, *Alosa*, and *Hyperlophus*.

References. Chapman (1944*b*), Day (1875), Fowler (1936), Misra (1953), Ridewood (1904*a*), Schultz *et al.* (1953), Whitehead (1963, 1963*a*), Woodward (1901, 1902–1912).

Material examined. Alosa pseudoharengus, one alizarin specimen, NMC60-452-A, Lake Ontario, Canada; *Clupea harengus pallasii*, four alizarin specimens, BC60-326, British Columbia; *Opisthopterus dovi*, alcoholic specimen, BC57-83, Bahia de Petacalco, Mexico.

CONGOTHRISSIDAE

Branchiostegals. 4 large and flat in *Congothrissa gossei* (3 on right side), all borne by the ceratohyal.

Hyoid arch. At least ceratohyal present.

Taxonomy. This family has just been erected by Poll (1964).

Reference. Poll (1964).

DENTICIPITIDAE

Pl. 10

Branchiostegals. 5 in *Denticeps clupeoides* with one epihyal and 4 ceratohyal, all external, the uppermost broad medially, the central 3 slender, the lowest broad with a clupeoid projection and bearing denticles along its anterior edge (other clupeiforms lack denticles). †*Palaeodenticeps* with 4 or 5, the upper 3 spathiform.

Hyoid arch. In *Denticeps* consists of interhyal, epihyal, ceratohyal, and two hypohyals. The lower hypohyal large, the upper small and located between the upper corners of the lower hypohyal and the ceratohyal.

Relationships. The keeled ventral scutes on the belly, the connection between the gas bladder and ear, and the clupeoid projection are all suggestive of clupeoid relationship. The reduction of caudal rays to 16 from the normal clupeoid number of 17 may represent an adaptation to miniaturization. Marshall (1962) also presents reasons for putting them in the same division (infrasuborder) with the Clupeidae and Chirocentridae. The fossil genus *Xenesthes* Jordan 1907, which Jordan placed in the Chirocentridae and then in the Xenesthidae amongst the Synentognathi, also had denticles on the bones of the skull.

References. Clausen (1959), Greenwood (1960).

Material examined. Denticeps clupeoides, one alizarin and two alcoholic specimens, uncatalogued NMC specimens from the Upper Yewa on the boundary between Nigeria and Dahomey, received through the kindness of Dr. Clausen; alcoholic specimen, USNM 195992, Nigeria.

Suborder **Bathylaconoidei**

BATHYLACONIDAE

Branchiostegals. 8–9 in *Bathylaco,* broad, curved, scythe-like with bases bearing anterior projections.

Relationships. Goode and Bean (1896) first placed *Bathylaco* in the Synodontidae of the Iniomi, probably largely on the basis of the elongate jaws and oblique opercular apparatus. Parr (1948) included it in the Isospondyli and regarded it as a possible intermediate between the Isospondyli and the Iniomi. Bertin and Arambourg (1958) recognized it as a suborder, Bathylaconoidei, intermediate between the Stomiatoidei and the Esocoidei.

The broadness of the branchiostegals differentiates the Bathylaconidae from the Myctophiformes and from any stomiatoid or esocoid. The comma-shaped preorbital photophore need not indicate relationship to the Stomiatoidei since similar photophores have arisen independently (in the Myctophiformes.) The anterior projections on the bases of the branchiostegals in Parr's figure are suggestive of the clupeoids and relatives. Amongst the clupeoids the engraulidids perhaps are the most similar with the narrow elongated toothed jaws, oblique suspensorium, and large anterior eyes. The Bathylaconidae are provisionally placed in the Bathylaconoidei. However, until specimens of *Bathylaco* are available for osteological study their status and placement will be uncertain.

References. Bertin and Arambourg (1958), Goode and Bean (1896), Jordan and Evermann (1896), Parr (1948).

Material examined. None.

†Suborder **Tselfatoidei**

Branchiostegals 11+ to 14 with about 4 epihyal and 9–10 ceratohyal, all apparently on the ventral edge of the hyoid arch. No gulars. Uppermost branchiostegals broader, lower ones slender. Operculum and suboperculum present and entire; interoperculum not known. Epihyal and ceratohyal known. A single fossil family.

The family Tselfatidae was founded by Arambourg (1954), who placed it in the Beloniformes. Bertin and Arambourg (1958) erected a new suborder, Tselfatoidei, for its reception in the Beloniformes. Patterson (1964) considered the Tselfatoidei unrelated to living Beloniformes or to any other teleostean order, but he left them amongst the Beloniformes. [*Protobrama* was placed in the Bramidae (Woodward, 1942). Patterson (1964) removed it to the Tselfatidae.] Several characters preclude the placement of the Tselfatidae in the Beloniformes: there are 18 caudal rays instead of 13; there are 7 pelvic rays instead of 6; the dorsal and anal are very long and high instead of small, low, and posterior; the parasphenoid and endopterygoid are toothed; the epihyal and ceratohyal are not sutured together; the operculars are entire; and the mouth is bordered by both the premaxillary and maxillary.

The entrance of the maxillary into the gape would permit placement in Clupeiformes, Notacanthiformes, Mormyriformes, Cypriniformes, or Anguilliformes. The numerous caudal rays, the normal anterior vertebrae, the toothed parasphenoid, the presence of a supraorbital, and the numerous distally spathiform branchiostegals preclude placement in any of these orders except the Clupeiformes. All the characters of the Tselfatidae are accommodated in the Clupeiformes except the long pedicels of the premaxillaries which might be protractile, a character normally acanthopterygian. But the majority of characters of the Tselfatidae would appear to place them among the primitive Clupeiformes, near the Elopoidei, Albuloidei, and Clupeoidei.

†TSELFATIDAE

Branchiostegals. Tselfatia with 13–14 slender branchiostegals which become spathiform dorsally. About 4 epihyal and 9–10 ceratohyal, distributed along the ventral edge of the hyoid arch. *Protobrama* has at least 11 slender branchiostegals.

Hyoid arch. Only epihyal and ceratohyal known. Epihyal and ceratohyal apparently not sutured together.

References. Arambourg (1954), Bertin and Arambourg (1958), Patterson (1964).

Material examined. None.

†Suborder **Saurodontoidei**

†SAURODONTIDAE

Branchiostegals. No information available.

Reference. Newton (1878).

Suborder **Hiodontoidei**, new suborder

Branchiostegals 7–10 with 2–2½ epihyal and 6–7 ceratohyal, 4–5 external and 4–5 on the ventral face of the hyoid arch. No gulars. Uppermost branchiostegals spathiform. Opercular bones complete and entire. Gill membranes separate. Two hypohyals. One living family.

Regan (1929) placed the Hiodontidae in a superfamily with the Notopteridae, to which it bears a superficial resemblance. Berg (1947) followed Regan but raised the superfamily to a suborder. Gosline (1960) placed the superfamilies Hiodontoidae, Notopteroidae, and Osteoglossoidae in a division Osteoglossi of the Clupeiformes. Greenwood (1963) has raised the division Osteoglossi to ordinal status.

However, the Hiodontidae seem to be well separated from the notopterids and osteoglossids by the following important characters: two hypohyals instead of one; upper branchiostegals spathiform instead of virgaform or acinaciform; 8 hypurals instead of four or fewer; 3–4 uroneurals instead of fewer; an adipose eyelid, a gular fold, and a postterminal centrum instead of none; nasals small instead of large. Although there is otic coupling of the gas bladder in both notopterids and hiodontids, the coupling is not similar and the divergence seems substantial (Marshall, 1962). All these characters combine to show that the Hiodontidae is distinct from the notopterid-osteoglossid group and is much more primitive. The origin of the Hiodontidae appears to lie with the elopoids, albuloids, or clupeoids. As in some clupeoids a duct from the gas bladder contacts the inner ear. The Hiodontidae differs from elopoids, clupeoids, and albuloids, however, in lacking oviducts, in having the parapophyses co-ossified with the centra, and in having 16 branched caudal rays. These characters justify its subordinal separation.

Hiodontidae (Hyodontidae)[1]

Branchiostegals. Vary from 7–10 in *Hiodon* (including *Amphiodon*). *Hiodon tergisus* 8–9 with 2 epihyal and 6–7 ceratohyal, 4 on the external and 4–5 on the ventral surface of the hyoid arch, the uppermost 2–3 branchiostegals spathiform and expanding distally. *Hiodon alosoides* 7–10, usually 9 with 2½ epihyal and 6½ ceratohyal, 5 on the external and 4 on the ventral face of the hyoid arch.

Operculars. Complete and entire. Gill membranes separate, with gular fold.

Hyoid arch. Interhyal, epihyal, ceratohyal, and two hypohyals in *Hiodon tergisus*.

References. Boulenger (1904), Jordan and Evermann (1896), Ridewood (1904, 1905*b*).

Material examined. Hiodon tergisus, alizarin specimen, BC58-164, Lake Winnipeg, Manitoba; alcoholic specimen, BC60-250, Lake Winnipeg, Manitoba; two alizarin specimens, NMC59-334 Lac St. Pierre, Quebec. *Hiodon alosoides*, one alizarin and ten alcoholic specimens, BC58-131, Saskatchewan River, Manitoba.

Suborder **Gonorhynchoidei**

Branchiostegals 4–5 with 4 epihyal and 0–1 ceratohyal, all external, the upper 2 spathiform. Opercular bones complete and entire. Gill membranes broadly joined to isthmus. Two hypurals. A single family.

Gosline (1960) united Berg's suborder Chanoidei, Phractolaemoidei, and Cromerioidei with the Gonorhynchoidei. At the same time he appeared uncertain that these groups belong together: "These five groups are so widely different that any relationship between them is difficult to comprehend. Yet the following similarities may be marshalled." He then lists gill membranes always attached to isthmus (yet in *Chanos* they are united and free), the mouth small and toothless or nearly so, supramaxillaries absent, the preopercular border free only below (*Chanos*), if at all, and several other characters. In his key he characterizes the suborder as having 3–4 branchiostegals; but Gonorhynchidae have 4–5.

I agree with Gosline that the Phractolaemidae, Kneriidae, and Cromeriidae belong in the same suborder. These families share the following characters: 1–3 branchiostegals, about 5–9 pelvic rays, 34–45 vertebrae, absence of axillary appendages, absence of pharyngeal teeth, restricted gill opening, scales cycloid or absent, presence of a gas bladder, and a similar caudal skeleton (Gosline). They are all small African freshwater fishes. The Chanidae share certain characters with these three families, such as 45 vertebrae, absence of pharyngeal teeth, cycloid scales, a gas bladder, a similar caudal skeleton (Gosline), but they differ in having 4 branchiostegals, 11–12 pelvic rays, axillary appendages, alar scales, and gill membranes united and free from the isthmus, and they are Indo-Pacific in distribution. However these differences are not too trenchant. Further, Audenaerde (1961) in his osteological study of *Phractolaemus* states that numerous osteological and anatomical characters suggest a close relationship of *Phractolaemus* and *Chanos*.

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[1] T. Cavender (Systematic position of the North American Eocene fish "*Leuciscus*" *rosei* Hussakof. Copeia (2): 311–320, 6 fig., 1966) names a new genus for *L. rosei*, *Eohiodon*, and places it in the Hiodontidae. It has about 10 branchiostegals. He believes that the caudal skeleton of *Phareodus* bridges some of the differences between hiodontids and living osteoglossiforms.

Gonorhynchidae shares only two of these characters with the three families: pharyngeal teeth absent and gill membranes joined to isthmus (but opening not restricted). It differs in having more branchiostegals, 10 pelvic rays, 54–56 vertebrae, axillary appendages, ciliated scales, no gas bladder, and a different caudal skeleton (Gosline) as well as in having peculiar characters such as a median rostral barbel, tongue-like and fringed flap-like structures on the roof of the mouth, rounded basi-branchial teeth, posterior side of fourth gill and back of branchial cavity papillose, black peritoneum, thick lips, and a pseudo-occipital condyle (Gregory, 1933). Gonorhynchidae is found in the Indo-Pacific. The characters shared with Chanidae are a high number of pelvic rays, axillary appendages, and number of branchiostegal rays (4 in Chanidae, 4–5 in Gonorhynchidae). But although the branchiostegal ray number is similar, as noted by Gosline, the branchiostegals differ markedly in arrangement and form. In Gonorhynchidae there are 4 on the epihyal, in Chanidae only 2. Those in Gonorhynchidae lack clupeoid projections and have a ridge, unlike those of Chanidae. The Gonorhynchidae have a large interhyal which is absent in the Chanidae, Phractolaemidae, and Kneriidae. The gill membranes differ in Gonorhynchidae.

It is concluded that Phractolaemidae, Kneriidae, Cromeriidae, and Chanidae belong in one suborder and that Gonorhynchidae require a separate suborder.

Gosline (1960) stated that the caudal skeleton of *Gonorhynchus* bore considerable resemblance to that of *Dussumieria*. The dussumieriids and alepocephalids are the only clupeoids with as many as 4 branchiostegals on the epihyal as in *Gonorhynchus*. The albuloids would also form a possible ancestor in this last respect, and they somewhat resemble *Gonorhynchus* in dentition.

GONORHYNCHIDAE

Branchiostegals. Vary from 4–5 in *Gonorhynchus*. The upper two branchiostegals broaden distally into a lamina and are more or less straight. A ridge strengthens each of the branchiostegals. Four branchiostegals on the epihyal and 0–1 on the ceratohyal, all on the external face of the arch.

Hyoid arch. Consists of large interhyal, epihyal, ceratohyal, and two hypohyals.

References. Hubbs (1920), Ridewood (1905*a*).

Material examined. Gonorhynchus gonorhynchus, alcoholic specimen, USNM 59920, New South Wales, Australia; alcoholic specimen, BC56-278, New Zealand; alizarin specimen, NMC62-140, South Africa.

Suborder Chanoidei

Branchiostegals 1–4 with 0–2 epihyal and 0–3 ceratohyal, all external, spathiform, with clupeoid projections (Kneriidae and Chanidae but not Phractolaemidae nor apparently Cromeriidae). Gular absent. Opercular bones complete and entire. Gill openings restricted or gill membranes united and free from isthmus (Chanidae). Two hypohyals (Kneriidae, Chanidae) or one (Phractolaemidae and Cromeriidae). An ossified interhyal absent, unlike other clupeiform suborders. Four families.

The relationships of this suborder are discussed under the Gonorhynchoidei. This suborder is distinguished from other clupeiforms by the absence of an ossified interhyal. The presence of a single hypohyal and the absence of clupeoid projections on the branchiostegals separate the Phractolaemidae and Cromeriidae from the other chanoids. It is possible that the presence of only a single hypohyal in some members and the absence of an ossified interhyal in all members are the results of neoteny.

CHANIDAE

Branchiostegals. In *Chanos* 4 branchiostegals on each side, all broad and spathiform but lower three tapering, bases broad with anterior clupeoid projection, 2 on epihyal, 2 on ceratohyal, all on external face of hyoid arch.
Hyoid arch. Consists of epihyal, ceratohyal, and two hypohyals. Interhyal absent; epihyal connected to hyomandibular by a ligament.
Relationships. The anterior projection at the base of the branchiostegal is similar to that in the clupeoids. The reflexed basicranium of *Chanos* is much like that of the Dussumieriidae.
References. Day (1875), Hubbs (1920), Jordan and Evermann (1896), Ridewood (1904*a*), Weber and de Beaufort (1913).
Material examined. Chanos chanos, alizarin specimen, BC60-25, Mexico.

KNERIIDAE (GRASSEICHTHYIDAE)

Pl. 10

Branchiostegals. Kneria 3 broadly spathiform branchiostegal rays with marked clupeoid projections, 1 epihyal and 2 ceratohyal, all external.
Hyoid arch. Consists of epihyal, ceratohyal, and two hypohyals. An interhyal was absent.
References. Berg (1947), Giltay (1934*a*), Hubbs (1920).
Material examined. Kneria sp., alizarin specimen, NMC64-235-S, Congo.

PHRACTOLAEMIDAE

Branchiostegals. 3 slender reported in *Phractolaemus*, but I have observed only one on the epihyal in two specimens of *P. ansorgei*; this one is rod-like except that it expands slightly at the distal tip like a spatula.

Hyoid arch. Interhyal apparently absent; epihyal, ceratohyal, and one hypohyal present.
Relationships. Like Mormyriformes, this family has only one hypohyal. However, the opercular and caudal skeleton differ strongly indicating that the loss of a hypohyal is only a parallelism.
References. Audenaerde (1961), Boulenger (1904), Hubbs (1920), Poll (1957), Ridewood (1905).
Material examined. Phractolaemus ansorgei, alizarin specimen, NMC64-236-S, Congo.

CROMERIIDAE

Branchiostegals. 3 slightly curved scimitar-like branchiostegals which insert on the ceratohyal.
Hyoid arch. Consists of epihyal, ceratohyal, and a single hypohyal. An ossified interhyal is absent, but d'Aubenton (1961, fig. 8) shows what he considers to be a cartilaginous interhyal fused to the hyomandibular.
References. d'Aubenton (1961), Gregory (1933), Hubbs (1920).
Material examined. None.

Suborder Stomiatoidei

Branchiostegals 5–24 with 0–1 interhyal, 3–8 epihyal, 4–12 ceratohyal, and 0–5 hypohyal, 3–12 external and 0–7 ventral. Gular absent. Opercular bones complete and entire. Gill membranes separate, united and free from isthmus, or joined to isthmus. Ceratohyal elongate, except in Sternoptychidae. Two hypohyals. Nine families, one wholly fossil, are placed in the family. Two additional families, one of which is fossil, are provisionally included.

The Rosauridae and Protostomiatidae are only provisionally placed in this suborder. Their branchiostegal series do not confirm placement here.

The remaining families share a number of characters and appear to form a natural phylogenetic unit. They are characterized by possession of numerous branchiostegals; by expansion of the upper one or two branchiostegals (except in Idiacanthidae), the remainder being slender; by the usual extending of the branchiostegals onto the lower hypohyal; by the deep and narrow operculum; by the reduced suboperculum and interoperculum; by the thin and poorly ossified opercular bones; and by the photophores on the branchiostegal membranes.

The high number of branchiostegals, the elongate mouth, and the deep operculum might lead one to conclude that the stomiatoids were derived from the Engraulididae. However, the stomiatoids have a higher number of branchiostegals on the epihyal, making such a derivation unlikely. The high number of epihyal branchiostegals would be commensurate with derivation from the elopoids. This contention is supported by Regan (1923*b*) who found striking agreement in the skulls of *Photichthys* and *Elops*.

The unusual feeding mechanism of Chauliodontidae and Malacosteidae is described and illustrated by Tchernavin (1948, 1953) and K. Günther and Deckert (1959).

GONOSTOMATIDAE (INCL. MAUROLICIDAE)

Branchiostegals. Vary from 7–21. *Agyripnus* 8–10, *Bonapartia* 11–16, *Cyclothone* 10–14, *Danaphos* 9–10, *Diplophos* 11–14, *Gonostoma* 10–14, *Ichthyococcus* 11–12, *Margrethia* 13, *Maurolicus* 9–10, *Neophus* 7–8, *Photichthys* 20–21, *Pollichthys* 11–12, *Sonoda* 8, *Triplophus* 11–14, *Valenciennellus* 9–10, *Vinciguerria* 10–12, *Woodsia* 17, *Yarella* 13–16. *Vinciguerria lucetia* 12 on both sides, with 4 epihyal, 7 ceratohyal, and 1 hypohyal, all external, the upper 2 broad and scimitar-like, the lower ones becoming progressively more rod-like. Photophores occur on the branchiostegal membranes of all genera.

Hyoid arch. Consists in *Vinciguerria* of interhyal, epihyal, long ceratohyal, and two hypohyals. Arch connected to mandibles by a membrane.

Relationships. The maurolicine genera, sometimes separated as a distinct family, have 7–10 branchiostegals, and the remainder have 10–21. This would support the phylogenetic divergence of the two groups.

Reference. Grey (1960).

Material examined. Vinciguerria lucetia, alizarin specimen, NMC61-195, 900 miles west of Lower California.

STERNOPTYCHIDAE

Branchiostegals. Vary from 5 to 11. *Argyropelecus* 9, *Polyipnus* 9–11, and *Sternoptyx* 5. *Argyropelecus* sp. 10 with 3 epihyal and 7 ceratohyal, 3 external and 7 ventral; the uppermost is a rounded triangle, the next two lath-like but expanding distally, the remainder rod-like. In *Sternoptyx* the upper branchiostegal is expanded and wing-like. The branchiostegal membranes bear photophores; 6 in *Polyipnus* and *Argyropelecus* and 3 in *Sternoptyx.*

Hyoid arch. Interhyal, long epihyal and ceratohyal, and two hypohyals present. The ceratohyal is bent in the middle with the apex uppermost in *Argyropelecus.* The arch is connected to jaws by a membrane.

References. Fowler (1936), Garman (1899), Gregory (1933), Jordan and Evermann (1896), Misra (1953), Schultz (1961), Weber and de Beaufort (1913).

Material examined. Argyropelecus sp., alizarin specimen, NMC61-184, 400 miles off California.

STOMIATIDAE

Branchiostegals. Vary from 14–19. *Stomias* 14–19; *Stomioides* 15.

Operculars. Complete and entire; gill membranes separate.

Hyoid arch. A membrane connects the lower jaw with the hyoid arch.

Relationships. Parr (1927) believed that the stomiatids deserved separation from the other two groups of stomiatoids, the gonostomatid group and the melanostomiatid group. This division is not reflected in the branchiostegal series.

References. Maul (1956*a*), Parr (1927, 1933), Regan (1923), Regan and Trewavas (1930), Weber and de Beaufort (1913).

Material examined. None.

CHAULIODONTIDAE

Branchiostegals. Vary from 15 to 21 in the genus *Chauliodus*. *Chauliodus macouni* 20 with 5 epihyal, 11 ceratohyal, and 4 hypohyal, the uppermost expanded, the remainder lath-like.

Hyoid arch. Interhyal, long epihyal and ceratohyal, two hypohyals. The hyoid arch and tongue are free from the jaws at the sides and are attached to the symphysis only by an elastic ligament. The resulting freedom enables the jaws to be shot forward and upward for ease in catching prey. Tchernavin (1948, 1953) reports on this interesting feeding mechanism.

References. Garman (1899), Morrow (1961).

Material examined. Chauliodus macouni, alizarin specimen, NMC61-192, 200 miles off Washington.

ASTRONESTHIDAE

Branchiostegals. Astronesthes 14–24.

Operculars. Complete and entire.

References. Fowler (1936), Gibbs and Aron (1960), Maul (1956*a*), Weber and de Beaufort (1913).

Material examined. None.

MALACOSTEIDAE

Branchiostegals. Vary from 8–18. *Malacosteus* 8 short, rod-like branchiostegals; *Aristostomias* 18 with one on the interhyal, 5 on the epihyal, and 12 on the ceratohyal, the upper two expanded slightly and lath-like, the remainder rod-like. Photophores on the branchiostegal membranes.

Hyoid arch. The hyoid arch is not connected to the front or sides of the mandible except by the long slender protractor hyoidei so that the mandible is completely free; hence the name loosejaws is applied to the family. Hyoid arch consists of interhyal, long epihyal and ceratohyal, and two hypohyals in *Aristostomias* and *Malacosteus*.

References. Fowler (1936), K. Günther, and Deckert (1959), Regan and Trewavas (1930), Weber and de Beaufort (1913).

Material examined. Aristostomias scintillans, alizarin specimen, NMC61-182, 50 miles west-southwest of Cape Flattery, Washington.

MELANOSTOMIATIDAE

Branchiostegals. Vary from 10–22 with 0–1 interhyal, 3–8 epihyal, 4–10 ceratohyal, and 0–5 hypohyal. *Tactostoma* 13 with 5 epihyal, 6 ceratohyal, and 2 hypohyal; *Bathophilus flemingi* 10 with 3 epihyal, 7 ceratohyal, and 0 hypohyal, 3 external and 7 ventral; *Bathophilus metallicus* 12 with 3 epihyal, 9 ceratohyal, and 0 hypohyal; *Chirostomias pliopterus* 22 with 8 epihyal, 10 ceratohyal, and 4 hypohyal; *Leptostomias bermudensis* 19 with 6 epihyal, 8 ceratohyal, and 5 hypohyal; *Echiostoma tanneri* 15 with 6 epihyal, 4 ceratohyal, and 5 hypohyal; *Melanostomias spilorhynchus* 13 with 4 epihyal, 5 ceratohyal, and 4 hypohyal; *Photonectes dinema* 15 with 5 epihyal, 6½ ceratohyal, and 3½ hypohyal; *P. margarita* 13 with 4 epihyal, 7 ceratohyal, and 2 hypohyal; *Flagellostomias boureei* 16 with 4 epihyal, 8 ceratohyal, and 4 hypohyal; *Grammatostomias flagellibarba* 13 with 5½ epihyal, 6½ ceratohyal, and 1 hypohyal; *Eustomias fissibarbis* 16 with 5 epihyal, 8 ceratohyal, and 3 hypohyal. In *Bathophilus flemingi* the upper branchiostegal expands into a lamina distally, the rest are lath-like; in *Tactostoma macropus* the upper one is expanded into an elongate triangle, the rest are styliform. In *Flagellostomias* and *Photonectes* the upper branchiostegal is branched, probably as a result of fusion of branchiostegals.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Bathophilus, Melanostomias, Photonectes*, and *Tactostoma*. Arch attached to mandibles by membrane.

References. Beebe and Crane (1939), Günther (1887), Parr (1933), Regan and Trewavas (1930).

Material examined. Bathophilus flemingi, alizarin specimen, NMC61-80, off northern California; *Tactostoma macropus*, alizarin specimen, NMC61-182, 50 miles west-southwest of Cape Flattery, Washington.

IDIACANTHIDAE

Branchiostegals. Vary from 12 to 18 in *Idiacanthus. Idiacanthus fasciola* 17 with 5 epihyal, 7 ceratohyal, and 5 hypohyal, all long and slender, the uppermost not expanded (unlike the preceding stomiatoid families).

Hyoid arch. Consists of interhyal, long epihyal and ceratohyal, and two hypohyals (basihyal of Beebe). Arch attached to mandibles by membrane.

Relationships. According to Beebe, closely related to the Melanostomiatidae. Differs from other stomiatoids by its lack of an expanded upper branchiostegal.

References. Beebe (1934), Garman (1899), Günther (1887), Regan and Trewavas (1930), Weber and de Beaufort (1913).

Material examined. None.

†TOMOGNATHIDAE

Branchiostegals. At least 7 in *Tomognathus mordax*, the dorsal one spathiform, the remainder slender, with about 45 on the epihyal.

Relationships. The deep operculum, the fact that only the uppermost of the branchiostegals is spathiform, and the high number (4–5) of branchiostegals on the epihyal suggest that this family is correctly placed in the Stomiatoidei.

Reference. Woodward (1902–1912, 1936).

†PROTOSTOMIATIDAE, *incertae sedis*

Branchiostegals. Vary from 10–24. †*Protostomias* about 24 short, slender branchiostegals; †*Pronotacanthus* 10 slender branchiostegals with 4 epihyal and 6 ceratohyal.

Hyoid arch. At least a long epihyal and a short ceratohyal in *Pronotacanthus*.

Relationships. Arambourg (1954) removed *Pronotacanthus* from the Notacanthidae and placed it in the Stomiatoidei. The operculum and the jaw apparatus of *Pronotacanthus* or *Prostomias* do not agree with those in other stomiatoids where the operculum is deep and narrow and the jaws and gape are long making the suspensorium vertical. The arrangement of the branchio-

stegals, the terminal mouth, and the absence of a 'spinous' dorsal in *Pronotacanthus* exclude it from the Notacanthidae.
References. Arambourg (1954), Woodward (1901).

ROSAURIDAE, *incertae sedis*

Branchiostegals. In *Rosaura rotunda* 10 long, slender branchiostegals which taper distally; about 4 epihyal and 6 ceratohyal; the uppermost is bent into an S-shape. Known only from a postlarval specimen of 8.4 mm. Branchiostegals extend out behind at right angles to the jaws, the rays continuing beyond the branchiostegal membrane.
Hyoid arch. At this stage consists only of an interhyal and a ceratohyal element which has not yet divided into epihyal, ceratohyal, and hypohyal.
Relationships. Tucker (1954) considered that the Rosauridae were most likely related to the stomiatoids, although the affinities were difficult to trace. The branchiostegals in Rosauridae project backwards horizontally, whereas in the stomiatoids they are between the jaws pointing towards the isthmus. Usually the upper branchiostegal of the stomiatoids is enlarged; in Rosauridae it is not enlarged. In these features *Rosaura* resembles the alepocephalids. Whereas the operculum of stomiatoids is elongate, forming most of the gill cover, it is quite reduced in Rosauridae and is no larger than the suboperculum. Because of the juvenile stage of the specimen and until more material is obtained it is difficult to come to conclusions on the relationships of Rosauridae. It is hence provisionally left, *incertae cedis*, in the Stomiatoidei, with the suggestion that it may be related to the alepocephalids.
Reference. Tucker (1954).
Material examined. None.

†Suborder **Enchodontoidei**

Branchiostegals about 9–16, slender. Gular absent. Operculars complete and entire. A single fossil family.

Gregory (1933) placed this family in the Iniomi. Berg (1947) includes it in the Clupeiformes. The slenderness of the upper branchiostegals and the great portion of the posterior border of the gill cover being taken up by the suboperculum are tendencies towards the iniomous condition. But the failure of the branchiostegals to curve behind the gill cover and the inclusion of the toothed maxillaries in the gape place the Enchodontidae in the Clupeiformes.

†ENCHODONTIDAE

Branchiostegals. Vary from about 9–16. *Halec* 9–15; *Enchodus* 12–16; *Eurypholis* about 15 slender attenuate branchiostegals, the upper apparently not spathiform; *Pantopholis* 14 narrow branchiostegals.
References. Davis (1887), Woodward (1901, 1902–1912).

Suborder **Salmonoidei**

Branchiostegals 2–19 with ½–4 on the epihyal, 0–7 on the ceratohyal, 2–6 on the external and 0–6 on the ventral surface of the hyoid arch. At least the upper branchiostegals spathiform. Gular absent. Opercular bones complete and entire (except operculum crenulate in *Bathylagus*, *Aplochiton*, and some Argentinoidea. Gill membranes separate or sometimes united and free from the isthmus. Two hypohyals present. Ten living families, plus one known only from fossils.

The Salmonoidei break down into three natural groups: the anadromous or freshwater Salmonoidea with 7–19 branchiostegals; the litophilus[1] and anadromous or freshwater Osmeroidea with 3–10 branchiostegals; and the offshore marine Argentinoidea with 2–6 branchiostegals. The Salmonoidea have two upturned postterminal vertebral centra, and the other two superfamilies have not more than one (Gosline, 1960). The branchiostegals and caudal structure both indicate that the Salmonoidea is the most primitive of the three groups. That the Salmonoidea, but not the others, possess an opisthotic and a supramaxilla is a further indication of their primitiveness.

The families here included in the Argentinoidea have been treated as a separate suborder Opisthoproctoidei by Chapman (1942, 1948). At the other extreme, Hubbs (1953) has suggested synonymizing the Macropinnidae, Dolichopterygidae, Bathylagidae, Microstomidae, Xenophthalmichthyidae, Opisthoproctidae, and presumably the Winteriidae with the Argentinidae. An intermediate path has been followed here, recognizing the affinities of the groups under a superfamily and yet retaining the distinctions of most of the groups by familial status. The families follow Cohen (1957).[2]

Superfamily SALMONOIDEA

Following the study of Norden (1961), Thymallidae and Coregonidae are synonymized with Salmonidae.

SALMONIDAE

Branchiostegals. Vary from 7–19 with 3–4 epihyal and 6–7 ceratohyal, 5 external and 6 ventral. *Oncorhynchus* 10–20. *Salmo* 9–13, *Salvelinus* 8–14, *Brachymystax* 10–13, *Hucho* 10–14, *Stenodus* 8–12, *Coregonus* 7–10, *Prosopium* 7–9, *Thymallus* 8–12. *Salmo clarkii* 11 with 4 epihyal and 7 ceratohyal, 5 external and 6 ventral, upper 4 broad and laminar, next 5 broad in the middle but narrowing at the ends, last 2 slender. *Thymallus arcticus* 9–10 with 3 epihyal and 6–7 ceratohyal. In a single sample of 50 *Oncorhynchus nerka*, seven were found with 11 branchiostegals, nineteen with 12, and twenty-four with 13.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Salmo*, *Salvelinus*, and *Thymallus*. In *Salmo* and *Thymallus* epihyal about two-thirds the length of ceratohyal.

Relationships. It may be stated that the number of branchiostegals does not give support to the separation of the families Coregonidae (7–12) and Thymallidae (8–12) from other Salmonidae (8–20). Norden (1961) is followed in reducing these to subfamilies. Norden (1961) considers that the Salmoninae is the most primitive subfamily. Its numerous branchiostegals support this view. The branchiostegal number would favour *Oncorhynchus* as being a primitive genus in the subfamily, but Norden (1961) considers it the most advanced. Branchiostegals indicate *Stenodus* to be the most primitive of the whitefishes, an indication in accord with its well-developed teeth.

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[1] Shelf-water loving (McAllister, 1963).

[2] Classification published in Cohen (1964. Suborder Argentinoidea. *In* Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res. (1), part 4: 1–70).

References. Berg (1949), Clemens and Wilby (1949), Dymond (1943), Hikita (1962), Holt (1960), Jordan and Evermann (1896), Kennedy (1943), Kimsey and Fisk (1960), Koelz (1929), McPhail (1961*a*), Miller (1950), Norden (1961), Rounsefell (1962), Vladykov (1954).

Material examined. Salmo clarkii, alizarin specimen, BC54-29, British Columbia; *Oncorhynchus nerka,* 50 alcoholic specimens, BC61-694, British Columbia; *Salvelinus namaycush,* skeletal specimens, NMC62-160-S, Ottawa fish market, and NMC60-100, Northwest Territories.

Superfamily OSMEROIDEA

Gosline (1960) included the Osmeridae, Plecoglossidae, Salangidae, Aplochitonidae, Retropinnidae, and Galaxiidae in this superfamily. He divided the superfamily into two groups with the first three families in a northern hemisphere group and the last three families in a southern hemisphere group.

OSMERIDAE

Pl. 10

Branchiostegals. Vary from 6–10. *Hypomesus* 6–8, *Mallotus* 8–10, *Osmerus* 6–8, *Spirinchus* 7–8, *Allosmerus* 6–7, and *Thaleichthys* 6–8. *Mallotus villosus* 9 with 4 epihyal and 5 ceratohyal, 5 external and 4 on internal face of hyoid arch, the uppermost spathiform, the lowest virgaform. *Osmerus eperlanus mordax* 7 with 4 epihyal and 3 ceratohyal, 4 external and 3 ventral, the uppermost broad and spathiform, the remainder becoming progressively narrow ventrally. In both these species there is a slight anterior projection at the base of the upper branchiostegal, reminiscent of the clupeoids. The upper branchiostegal is only slightly curved in the family.

Hyoid arch. An interhyal, epihyal, ceratohyal, and two hypohyals in *Thaleichthys*, *Mallotus*, and *Osmerus*. The epihyal large, nearly as long as the ceratohyal in these genera.

References. Chapman (1941*a*), McAllister (1963).

Material examined. Osmerus eperlanus mordax, alizarin specimen, NMC62-110, Great Lakes, Canada; *Mallotus villosus,* alizarin specimen, NMC60-47, Yukon, Canada; also material listed in McAllister (1963).

†THAUMATURIDAE

Branchiostegals. More than 5 in *Thaumaturus.*

Hyoid arch. At least ceratohyal and epihyal present.

Relationships. Generally associated with the Salmonidae. The known number of branchiostegals is lower than in the Salmonidae; however, the series may be incomplete. Norden's (1961) suggestion from the caudal vertebra of

Thaumaturus, that it is allied to Argentinidae or Osmeridae, would agree with the known number of branchiostegals. That it is known from freshwater deposits favours the latter. But I (MS.) suggest that the Thaumaturidae are not closely related with the Osmeridae, now published, Can. Field-Nat. 80(4).
Reference. Voigt (1934).

PLECOGLOSSIDAE

Branchiostegals. Plecoglossus 5–6 with 2½ on the epihyal and 3½ on the ceratohyal, 3 external and 3 on the ventral face of the hyoid arch. The upper three are broad, spathiform, and crescentic, the lower three narrow.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal about three-quarters the length of ceratohyal.
Relationships. The number and arrangement of the branchiostegals agree with the Osmeridae although there are generally more branchiostegals in the Osmeridae. The upper branchiostegal in Osmeridae is only very slightly curved whilst in the Plecoglossidae it is distinctly crescentic. Further, the interoperculum is normally exposed in Osmeridae whereas in the Plecoglossidae it is hidden by the preopercle.
References. Chapman (1941), Okada (1960).
Material examined. None.

SALANGIDAE

Branchiostegals. 4 in *Salangichthys* and reported for the family.
Relationships. In the reduced number of branchiostegals, lack of scales, and neotenous condition the Salangidae differ from the other northern Osmeroidea.
References. Gosline (1960), Hubbs (1920), Okada (1960), Wakiya and Takahasi (1937).

RETROPINNIDAE

Branchiostegals. 5–6 in *Retropinna*. Upper branchiostegal broad and spathiform.
Reference. Stokell (1941).
Material examined. Retropinna osmeroides, two alcoholic specimens, BC56-296, Ashley River, New Zealand.

GALAXIIDAE

Branchiostegals. Vary from 5–9. *Galaxias* with 5–9, *Neochanna* with 6–7. *Galaxias maculatus* 5 with 2 epihyal and 3 ceratohyal, 3 on the external and 2 on the ventral face of the hyoid arch, the upper three spathiform. *G. attenuatus* 8 with 3 on the external face of the epihyal and 5 on the ventral ceratohyal, upper three spathiform. *Neochanna apoda* 6 with 2 epihyal and 4 ceratohyal, 3 on the external and 3 on the ventral face of the hyoid arch, the upper three broad laminar, spathiform, the lower three slender. *Galaxias indicus* with 9. The upper spathiform branchiostegals hastate in form.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. The epihyal is about one-half as long as the ceratohyal.

References. Gregory (1933), Misra (1953), Stokell (1949).

Material examined. *Galaxias maculatus*, alizarin specimen, SU 22679, Mayne Harbor, Patagonia; *Neochanna apoda*, alizarin specimen, BC56-288, Wairarapa district, New Zealand; *Galaxias attenuatus*, alizarin specimen, NMC62-244, Hinds River, New Zealand.

APLOCHITONIDAE (HAPLOCHITONIDAE)

Branchiostegals. Vary from 3–6. *Aplochiton zebra* 3 with ½ epihyal and 2½ ceratohyal, 2 external and 1 on ventral face of the hyoid arch, all broad spathiform, straight; *Lovettia* 6.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal about two-fifths the length of ceratohyal.

References. Chapman (1944*a*), Gosline (1960), Hubbs (1920).

Material examined. None.

Superfamily ARGENTINOIDEA

The classification of Cohen (1957) is followed for this group.

ARGENTINIDAE (incl. MICROSTOMIDAE and XENOPHTHALMICHTHYIDAE)

Branchiostegals. Vary from 3–7. *Argentina* 5–7, *Glossanodon* 4–5, *Nansenia* 3–4, *Microstoma* 3–4, *Xenophthalmichthys* 3. *Argentina sphyraena* 7 with 2 epihyal and 5 ceratohyal, 3 on the external face and 4 on the ventral edge of the hyoid arch, the upper 3 broadly spathiform, the rest slender. *Xenophthalmichthys danae*, 3 spathiform branchiostegals on the external face of the arch.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Argentina* and *Nansenia*.

Relationships. According to the number of branchiostegals, this family (particularly the Argentininae) would be the most primitive of the superfamily. It is the only family of the superfamily with a postcleithrum, and it has the most numerous pelvic rays. This would confirm the indication given by the branchiostegals. Cohen (1957) has already stated this position.

References. Bertelsen (1958), Bertin and Arambourg (1958), Chapman (1942, 1942*a*, 1948), Cohen (1957, 1958*a*, 1958*b*), Jensen (1948), McAllister (1961), Regan (1925*a*).

Material examined. *Argentina silus*, four alcoholic specimens, NMC62-79, southwest of Sable Island, Nova Scotia.

BATHYLAGIDAE

Branchiostegals. Constantly number 2. *Leuroglossus* 2, *Bathylagus* 2. Two external epihyal: in *B. pacificus* they are broad, with the breadth exceeding one-third the length; in *glacialis* they are slender, with the breadth less than one-tenth the length. Cohen (1957) indicates that Beebe was in error in giving a count of 3–4 for *Bathylagus* and states that he has never seen only one branchiostegal as was reported by Hubbs (1920). But Hubbs was not in error; he stated only that there was a single *large* branchiostegal and did not imply that there was not a further slender one below.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Bathylagus*. Beebe mislabels the hypohyals as basihyal.

References. Beebe (1933), Bolin (1938), Chapman (1943), Cohen (1957, 1958*c*), McAllister (1961).

Material examined. Bathylagus milleri, alizarin specimen, NMC61-183, 100 miles off north end of Vancouver Island, B.C.

OPISTHOPROCTIDAE (DOLICHOPTERYGIDAE, WINTERIIDAE, MACROPINNIDAE)

Branchiostegals. Vary from 2–4. *Rhynchohyalus* 4, *Macropinna* 3, *Dolichopteryx* 2, *Bathylychnops* 2, *Opisthoproctus* 2. *Macropinna* 3 spathiform branchiostegals on the lower external face of the unossified epihyal.

Hyoid arch. In *Macropinna* consists of interhyal, epihyal, ceratohyal, and two hypohyals. The epihyal is ossified only on its dorsal edge.

Relationships. The branchiostegals of *Dolichopteryx* definitely support its placement in the Opisthoproctidae rather than in the Alepocephaloidea (in which group it had been placed). (*See* Note 3, Addenda.)

Suborder **Esocoidei**

Branchiostegals 4–20 with 1–8 epihyal and 3–10 ceratohyal, 3–8 on the external and 1–10 on the ventral face of the arch. Branchiostegals acinaciform or spathiform. Gulars absent. Opercular bones complete and entire. Gill membranes separate. Two hypohyals. Four families, one extinct.

The number of branchiostegals would indicate the Esocidae (and †Palaeoesocidae) to be more primitive than the Umbridae and Dalliidae. But according to Gosline (1960), the caudal skeleton of *Umbra* seems more primitive than that of *Esox*. Other characters were therefore considered in Chapman (1934) in an attempt to determine which family was most primitive: the number of pelvic rays, caudal rays, and actinosts; the presence of a postcleithrum, myodome, inframandibular, suborbitals, nasal, septomaxillary, and basisphenoid; the presence of ribs on anterior vertebrae; and the reduction of the preorbital. The Esocidae were found most primitive, followed by the Umbridae and lastly the Dalliidae. In this case most characters are in agreement with the number of branchiostegals (and not the caudal skeleton) in demonstrating the Esocidae to be more primitive.

The number of branchiostegals in the Palaeoesocidae is about the same as in the Esocidae. *Palaeoesox* further agrees with the Esocidae and differs from the Dalliidae and Umbridae in that it has suborbitals and nasals, thus confirming the relationships suggested by the branchiostegals.

The Esocidae and Palaeoesocidae on one hand, and the Dalliidae and Umbridae on the other hand, are quite divergent in the number of branchiostegals (10–20 as opposed to 4–8) and in the suborbitals, nasals, inframandibulars, and so on. Therefore it seems unwise to place the Palaeoesocidae in the Umbroidea; they are here placed provisionally in the Esocoidea.

The large number of branchiostegals, many of which are on the epihyal, suggests that the esocoids are descended from the elopoids or primitive clupeoids, perhaps not greatly distant from the stock that gave rise to the stomiatoids. Frost (1926) notes that the sagitta of *Esox* resembles that of *Megalops* but is more highly specialized.

Superfamily ESOCOIDEA

ESOCIDAE

Branchiostegals. Vary from 10–20 in *Esox* with 5–8 epihyal and 7–10 ceratohyal, 5–8 external and 7–10 internal or ventral. All the rays are acinaciform. Crossman (1960) presents large samples showing variability within the species.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. The epihyal is about two-thirds the length of the ceratohyal. Two small prongs extend towards the hypohyals from the upper anterior end of the ceratohyal.
References. Berg (1949), Crossman (1960).
Material examined. Esox masquinongy, alizarin specimen, NMC60-219, Ontario.

†PALAEOESOCIDAE

Branchiostegals. 13 branchiostegals in *Palaeoesox fritzschi* with 6 on the external face of the epihyal and 7 on the inner face of the ceratohyal. Branchiostegals acinaciform.
Hyoid arch. At least ceratohyal and epihyal present.
Relationships. In shape, number, and distribution of the branchiostegals Palaeoesocidae agree with the Esocidae and differ from the other two families.
Reference. Voigt (1934).
Material examined. None.

Superfamily UMBROIDEA

UMBRIDAE

Branchiostegals. Vary from 4–7. *Umbra limi* 4–5 with 1 epihyal and 3–4 ceratohyal, 3 external and 1–2 ventral. The upper two are crescentic, the lower ones are slender. *Novumbra hubbsi* 6–7 with 2–3 on the epihyal and 4–5 on the ceratohyal, 4–5 external and 2 ventral.
Hyoid arch. Interhyal, epihyal, ceratohyal, and two hypohyals in *Umbra* and *Novumbra*. In *Umbra* the dorsal edge of the ceratohyal sends two prongs towards the hypohyals; the epihyal is about two-fifths the length of the ceratohyal.
References. Berg (1949), Chapman (1934), Dineen and Stokely (1954).
Material examined. Umbra limi, five alizarin specimens, NMC60-486-A, Bruce Co., Ontario; five alizarin specimens, NMC62-135, Ottawa, Ontario; five specimens, BC59-199, Silver Lake, Ontario.

Superfamily DALLIOIDEA

DALLIIDAE

Pl. 10

Branchiostegals. Vary from 7–8 in *Dallia* with 3 epihyal and 4–5 ceratohyal, 5 external and 2–3 internal. All acinaciform as in Esocidae.
Hyoid arch. Consists of interhyal, epihyal, dumbbell-shaped ceratohyal, and 2 hypohyals. Dorsal edge of anterior end of the ceratohyal sends 2 prongs towards the hypohyals. The epihyal is about one-third the length of the ceratohyal.
References. Berg (1949), Chapman (1943).
Material examined. Dallia pectoralis, two alizarin specimens, NMC62-244, tributary to Tokotna River, Alaska.

Order NOTACANTHIFORMES (HALOSAURIFORMES)

Pl. 9

Branchiostegals 6–23 with 4–7 on the epihyal and 2–7 on the ceratohyal, all erupting from the external face of the hyoid arch; all acinaciform; gulars absent; opercular bones without spines and complete; interhyal, epihyal, ceratohyal, and two hypohyals present. Epihyal and ceratohyal not sutured. Gill membranes separate. Upper Cretaceous to present. Three families.

Regan (1929) placed the three families in the same order, and Berg (1947) placed the Halosauridae in a separate order; but most authors, such as Bertin and Arambourg (1958), Bailey (1960), and Marshall (1962), have not followed Berg. The results of this study support uniting the families in a single order.

The families share numerous fairly straight (internal characters not known for Lipogenyidae) acinaciform branchiostegals erupting from the external face of the hyoid arch, needle-like teeth (absent in Lipogenyidae), numerous pelvic rays (7–11) some of which may change into spines, abdominal and close or fused pelvics, elongate anal fin, physoclistic gas bladder, maxillary spine (not all Halosauridae), a peculiar interoperculum with a projection extending back to the suboperculum, small cycloid scales, elongate snout with inferior mouth, and so on. The peculiar spines of the Notacanthidae and Lipogenyidae may be regarded as independently evolved and not derived from those in the acanthopterygian fishes (*See* Marshall (1962) for a full discussion).

Confirming the primitiveness of these fishes, that they are malacopterygian in nature and that the spines must be an independent development, are the following characters: the absence of a retractores arcuum branchialium muscle[1]; the numerous branchiostegal rays on the lateral face of the hyoid arch (not in the 4 + X pattern), the numerous pelvic rays, the failure of the premaxillary to exclude the maxillary in Halosauridae, the lack of suturing between the epihyal and ceratohyal, the inner pelvic radial of ispondylous type (Gosline, 1961), and the cycloid scales. It is evident then that the Notacanthiformes are malacopterygians. Further, their characters permit them to be derived only from the primitive Clupeiformes. The most likely ancestral group in the Clupeiformes appears to be the elopoid ancestors of the Albuloidei. The Albuloidei have numerous branchiostegals on the external surface of the hyoid arch, 2 hypohyals, 1 supramaxillary, 10–14 pelvic rays, inferior mouth with toothless maxillary, needle-like teeth, long snout, perforated premaxillary, and membranous cavernous suborbitals (absent in Notacanthidae), all of which suggests derivation of the Notacanthiformes from the elopoid ancestors of the Albulidae. According to Frost (1926) the sagitta of *Halosaurus* is of the elopine type. The cartilaginous shelf of the ceratohyal on which the branchiostegals rest in *Aldrovandia affinis* may represent the bony shelf seen in *Albula*. Marshall (1962) points out characters shared with the Anguilliformes and suggests affinity to them.[1]

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[1] *See* Holstvoogd, footnote 2, p. 33.

The more numerous branchiostegals, absence of fin spines, mouth bordered by premaxillary and maxillary, and presence of a supramaxillary indicate that the Halosauridae is the most primitive family in the group. However, it does have some specializations such as a ventral lateral line (which might be associated with a suggested function of the lateral line, the bearing of photophores). The Lipogenyidae is little known and is apparently represented by only one specimen, characterized by the presence of several rays in the short dorsal fin, the absence of teeth, and the separation of the two rami of the lower jaw. Whereas the latter might be a teratological condition, the condition of the dorsal fin is both distinctive and intermediate between those of the other two families. Although the dorsal fin is intermediate, most of the characters are closest to those of the Notacanthidae.

Halosauridae

Branchiostegals. Vary from 9–23 with 4–5 on the epihyal and 5–7 on the ceratohyal, all on the external face of the hyoid arch, all acinaciform. *Halosaurus* 11–23, *Aldrovandia* 9–12, †*Echidinocephalus* about 12. *Aldrovandia affinis* (as in *Halosauropsis*) 10 with 5 epihyal and 5 ceratohyal, all acinaciform, the upper ones with a small, thin blade on either side of the base, the lowest three resting on the external surface of a cartilaginous shelf projecting down from the lower side of the middle of the ceratohyal. *Aldrovandia macrochir* 11 with 4 epihyal and 7 ceratohyal, all on the external face of the arch, all virgaform. *Halosaurus oweni* 11 with 5 epihyal and 6 ceratohyal, all on the external face of the arch, all acinaciform (Günther reports 14 for this species; it may be that branchiostegals were lost from the skeletal specimen here examined; alternatively this specimen may be misidentified).
Operculars. Marshall (1962) has corrected Günther's interpretations of the operculars. In *Aldrovandia affinis* operculum entire, interoperculum elongate lying under the preoperculum and extending from the jaw back to the suboperculum. The suboperculum small.
Hyoid arch. In *Aldrovandia macrochir*, *A. affinis*, and *Halosaurus oweni* con-

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[1] Giles W. Mead reports leptocephalus larvae for the order and concludes a close relationship of the Notacanthiformes with the eels must be recognized (1965. The larval form of the Heteromi (Pisces). Breviora (226): 1–5, 1 fig.). *See also* Harrisson, C.M.H. 1966. On the first halosaur leptocephalus: from Madeira. Bull. British Mus. (Nat. Hist.), Zool. 14 (8): 441–486, 1 pl., 6 text-fig.

sists of interhyal, epihyal, ceratohyal. The number of hypohyals is unknown. Epihyal one-half to two-thirds the length of the ceratohyal. Ceratohyal dumbbell-shaped.

Relationships. The generic classification above follows Norman (MS.). The branchiostegals would tend to affirm this generic separation. There are 12–23 in *Halosaurus* and 9–12 in *Aldrovandia* (assuming the count of 11 for *Halosaurus oweni* to be incorrect). That *Halosaurus* lacks prominent lateral ridges on the head and has unenlarged lateral line scales would seem to indicate that it is more primitive than *Aldrovandia.* The suggested relationship is in accordance with the higher number of branchiostegals in the genus *Halosaurus.* The Cretaceous *Echidnocephalus* is very similar in branchiostegals and other characters to present day *Halosaurus.* In Woodward (1901) the *Enchelurus syriacus* specimen P9168 and the *E. anglicus* specimen P4249 may be halosaurids, but the *Enchelurus syriacus* specimen P5998 appears, from the conformation of its suboperculum and skull, to be a primitive anguilliform.

References. Garman (1899), Goode and Bean (1896), Günther (1887), Jordan and Evermann (1896), Marshall (1962), Weber and de Beaufort (1922), Woodward (1897).

Material examined. Aldrovandia (as *Halosauropsis*) *affinis*, alcoholic specimen, arch and branchiostegals dissected out and stained, SU 23199, *Albatross* station 4971; *Aldrovandia* (as *Halosaurus*) *macrochir*, skeletal specimen, USNM 26949, 36° 34′ N, 73° 48′ W; *Halosaurus oweni*, skeletal specimen, USNM 26711, 39° 29′ N, 71° 46′ W.

LIPOGENYIDAE

Branchiostegals. Unknown.

Relationships. (*See above* ordinal discussion.)

References. Goode and Bean (1896), Jordan and Evermann (1896).

Material examined. None.

NOTACANTHIDAE

Pl. 9

Branchiostegals. Vary from 6–13. *Notacanthus* (8) 9–13, *Polyacanthonotus* 9, and *Macdonaldia* 6. *Notacanthus phasganorus* 9 with 4 epihyal and 5 ceratohyal, all on the external surface of the arch, all slender acinaciform (both in skeletal and alizarin specimens). In Günther's figure of *Notacanthus sexspinis* there appear to be 9 with 7 epihyal and 2 ceratohyal; this arrangement should be checked.

Hyoid arch. Consists in *Notacanthus* of interhyal, epihyal, ceratohyal, and two hypohyals. The ends of the hyoid bones are cartilaginous. The portions that are ossified are only weakly ossified, judging by the weak absorption of alizarin. The ceratohyal is dumbbell-shaped. The epihyal is about one-quarter the length of the ceratohyal (shorter than in *Halosaurus*).

Relationships. Pronotacanthus has been removed and placed in the †Prostomiatidae by Arambourg (1954).

References. Fowler (1936), Garman (1899), Günther (1887), Jordan and Evermann (1896), Maul (1955), Tucker and Jones (1951).

Material examined. Notacanthus phasganorus, one skeletal and one alizarin specimen, NMC62-133, off Newfoundland, at 43° 32′ 00″ N, 48° 48′ 00″ W.

Order MORMYRIFORMES (OSTEOGLOSSIFORMES, NOTOPTERIFORMES[1])

Branchiostegals 3–17 with 0–5 epihyal and 1–8 ceratohyal, 4–15 external and 0–5 ventral, acinaciform or virgaform, sometimes spathiform. Gular absent.[2] Operculum present and entire or crenulate; suboperculum entire, if present; interoperculum present and entire. One hypohyal (above, except perhaps in *Arapaima*) or none. Ceratohyal, epihyal, and interhyal (sometimes tendon-like) usually present (latter may be absent or may not be ossified). Gill membranes joined to isthmus, joined together and free from isthmus, or (in one family) separate. Eight families, one known only from fossils. Upper Cretaceous to present.

Berg (1947) placed the osteoglossoid families (including Notopteridae and Hiodontidae) in the Clupeiformes and the mormyroid families in the Mormyriformes. Gregory (1933) placed these two groups in adjacent superfamilies in the Clupeiformes, as did Regan (1929). Gosline (1960) placed the osteoglossoid families with the notopterids and hiodontids in their own division, Osteoglossi, separating them from all other clupeiform fishes, which he placed in the division Clupei. Greenwood (1963) has raised the Osteoglossi to the status of an order.

The basic similarities in the branchial skeleton of the osteoglossoid- and mormyroid-type families suggest that they belong in the same group. That they differ by these same characters from the Clupeiformes further suggests that the osteoglossoid and mormyrid families be placed together in the same order, Mormyriformes. The Mormyriformes (used from here on in the expanded sense including the notopteroid, osteoglossoid, and mormyroid families which are dealt with below) thus differ from all Clupeiformes investigated (except the peculiar Cromeriidae and Phractolaemidae) in having 0–1, instead of 2, hypohyals. The branchiostegals of Mormyriformes tend to be rectilinear and slender whilst at least the upper ones of Clupeiformes are usually broad and laminar. Gosline (1960) has indicated that the families here placed in Mormyriformes are peculiar in having a single postterminal centrum, the other postterminal centrum being fused with a hypural in such a way that the resultant element is horizontally oriented. They have fewer (16 or less) than the usual number of branched caudal rays in the Clupeiformes (17). Other common characters of the osteoglossoid and mormyroid families are the absence of pharyngeal teeth (Poll, 1957; Boulenger, 1909) and the absence of a supramaxillary; the usual presence of an orbitosphenoid; the co-ossification parapophyses with centra; the tendency towards fusion of the premaxillaries; the meeting of the parietals; and a rigidly enclosed nasal capsule (Gosline, 1961) without diverticula and without supraorbital bone, the place of the latter being taken by a canal-bearing antorbital (?) that fuses with the frontal.

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[1] Mednikov, B.M. 1962. Bull. Moscow Soc. Nat. 67: 155–156.

[2] But Gosline (1965, Copeia (2): 186–194) observed a developed median gular in *Osteoglossum*. This would support, as is herein suggested, derivation of the Osteoglossiformes from the Elopoidei or an advanced holostean.

The osteoglossids, notopterids, and mormyrids also share a peculiar ceratohyal shelf on which the branchiostegals insert (somewhat as in *Albula* and *Amia*) and (Marshall, 1962) a distinctive gas bladder. Only *Notopterus* and *Gymnarchus* are known to possess a completely closed adult system of cephalic sensory canals (Kapoor, 1964). *Heterotis* provided the only scales known to Cockerell (1910), outside of the Mormyridae, that had the true mormyrid form and pattern.

The Hiodontidae were included by Gosline (1960) in his division Osteoglossi and by Greenwood (1963) in his Osteoglossiformes. As shown under that family, the Hiodontidae differ trenchantly from the Mormyriformes and should be placed in their own suborder among the Clupeiformes.

Berg (1947) included the Mormyridae and Gymnarchidae in the Mormyriformes and excluded the osteoglossoids and notopteroids. He considered this order one of the best characterized, evidently on the basis of the well-developed cerebellum. But the cerebellum is differently developed even in these two families. Neither can the electric organs (with which the large cerebellum may be associated) be considered of ordinal value, as they occur *in* certain family group taxa such as Electrophorinae and Malapteruridae of the Cypriniformes. It is therefore with little hesitation that the limits of the Mormyriformes are enlarged, especially since several independent morphological characters, particularly the hyoid arch and caudal skeleton, indicate such a change.

Branchiostegal form and number would agree with the derivation of the Mormyriformes from the Elopoidei. McEwen (1938) concludes that the form and arrangement of visual elements of the Mormyridae are most similar to those of *Elops* and *Megalops*. (*Hiodon*, it may be noted, differs from the Mormyridae in lacking cones—Moore and McDougal, 1949.) Mr. T. Cavender has kindly permitted me to examine his manuscript, 'Systematic position of the American Eocene fish, "*Leuciscus*" *rosei* Hussakof,'[1] describing the tail of an Eocene osteoglossoid, *Phareodus*, which is unlike those of living Mormyriformes. The tail structure is considered to bridge the major structural differences between the caudal skeletons of hiodontids and modern osteoglossoids. However, known Clupeiformes have two hypohyals (except two chanoids) and lack lateral parasphenoid processes, unlike the osteoglossoids.

The last two characters (single hypohyal, parasphenoid processes) are present in the Leptolepiformes. Some lower orders also possess lateral parasphenoid processes, but these, unlike the Mormyriformes and Leptolepiformes, lack intermuscular bones. This evidence strongly suggests that the Leptolepiformes may be ancestors of, or close to the ancestors of, the Mormyriformes.[2] If this were so it would make the Malacopterygii a more homogeneous group (the Mormyriformes would then be placed in the Holostei). It is unlikely that the parasphenoid processes of the osteoglossoids are a recent parallel development since they are present even in the Eocene osteoglossoid, *Phareodus* (Mr. Harold Roellig of the American Museum of Natural History kindly permitted me to check this feature from his unpublished drawings; he also supplied me with branchiostegal counts for this genus).

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[1] Now published in Copeia (2): 311–320, 1966.

[2] Bridge (1895) was the first to point out that the parasphenoid processes were shared by *Osteoglossum* and the holosteans; he also pointed out that *Osteoglossum* and *Lepisosteus* have the same peculiar type of tongue invested with parallel rows of bony plates. But he considered these similarities to be parallelisms. But *see* p. 34 re intermuscular bones.

Gosline (1965, Copeia (2): 186–194) believes that the Teleostei is monophyletic, but "that if any teleostean group evolved independently, it is the hiodontid-osteoglossoid-mormyroid lineage. . . ."

Suborder **Osteoglossoidei (Pantodontoidei)**

The Osteoglossidae and Arapaimidae appear to be more primitive, having a suboperculum, a roof to the posttemporal groove, and 10–17 branchiostegals; the Pantodontidae and Heterotidae lack a suboperculum and a roof to the posttemporal groove and have only 7–8 (9?) branchiostegals. The four families are united by a unique character: the entopterygoid articulates with the lateral peg of the parasphenoid in a manner unknown in other fishes (Ridewood, 1905). The completeness of the opercular apparatus suggests that the fossil Plethodidae might be related to the Osteoglossidae and Arapaimidae, although the small number of branchiostegals disagrees with this allocation. Greenwood and Thompson (1960) lump the following families under Osteoglossidae.

The reduction of branchiostegals in the Heterotidae might be related to the presence of a respiratory organ on the fourth branchial arch.

OSTEOGLOSSIDAE

Branchiostegals. Branchiostegals vary from 10–17. †*Dapedoglossus* at least 10; †*Brychaetus* at least 15; †*Phareodus* 11 (*fide* Harold F. Roellig); *Osteoglossum* 10–11; *Scleropages* 13–17. *Osteoglossum bicirrhosum* 11 with 3 epihyal and 8 ceratohyal, 8 on external and 3 on ventral face of hyoid arch, the upper three spathiform, the lower ones becoming virgaform. *Scleropages formosa* (right side) 14 with 2 epihyal and 12 ceratohyal, all external, upper three spathiform.

Operculars. Complete but suboperculum small.

Hyoid arch. Consists of one triangular hypohyal (above), ceratohyal (broadened convexly on ventral side in *Scleropages*), and epihyal, and interhyal.

Relationships. Poll (1957) includes the Heterotidae in this family. However, the Heterotidae are distinguished by the possession of an epibranchial organ and fewer branchiostegals, 7–9 instead of 10–17.

References. Norman (MS), Poll (1957), Ridewood (1905), Weber and de Beaufort (1913), Woodward (1901).

Material examined. Osteoglossum bicirrhosum, alcoholic specimen, BC60-162, South America; *Scleropages formosa,* alcoholic specimen, NMC63-296, Pahang, Malaysia.

ARAPAMIDAE

Branchiostegals. Arapaima gigas 10–11 with 5 epihyal and 5–6 ceratohyal. The upper ones are larger, slightly expanded, and lamellate, and the lower ones are more slender and rod-like. Several other authors (*in* Ridewood, 1905) place the number at 16.

Operculars. Complete but suboperculum small.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and one hypohyal, probably the equivalent of the lower according to Ridewood. If this is so, then

Arapaimidae differ from the other osteoglossoid families (which possess a mainly dorsal hypohyal).
Reference. Ridewood (1905).
Material examined. None.

†PLETHODIDAE (NIOBRARIDAE)[1]

Branchiostegals. About 6 in *Anogmius.*
Operculars. Complete and entire. Operculum subtriangular and heavy; preoperculum expanded ventrally and may have covered the interoperculum.
Reference. Woodward (1899, 1901, 1902–1912).
Material examined. None.

PANTODONTIDAE

Branchiostegals. Pantodon buchholzi 8 (9?), virgaform and almost straight. The two slender arms of the interoperculum have been mistaken for two branchiostegal rays giving rise to counts of up to 11 for this species.
Operculars. Operculum entire, interoperculum V-shaped, and suboperculum absent. Gill membranes separate. The two ray-like arms of the interoperculum have been mistaken for branchiostegals, the juncture of the two arms basally having been unobserved previously.
Hyoid arch. A large ossified interhyal, an epihyal, a ceratohyal, and a small hypohal (above) present.
References. Berg (1947), Boulenger (1909), Ridewood (1905).
Material examined. Pantodon buchholzi, alizarin specimen, NMC64-234-S, central Congo.

HETEROTIDAE

Branchiostegals. Heterotidae 7–9. *Heterotis niloticus* 8 with 3½ epihyal and 4½ ceratohyal. Of the epihyal branchiostegals the dorsal one lies halfway up the outer face of the epihyal, the lower two lie on the lower edge of the epihyal, and the next one lies on the epihyal-ceratohyal border. The upper three are spathiform, the lower five are virgaform.
Operculars. Operculum large and entire; interoperculum entire. Suboperculum not observed by Ridewood but definitely reported by Valenciennes (*in* Ridewood) as a very small bone. Greenwood and Thompson report a suboperculum.
Hyoid arch. Epihyal, ceratohyal, and a small hypohyal (above) known.
References. Greenwood and Thompson (1960), Poll (1957), Ridewood (1905).
Material examined. None.

Suborder Notopteroidei

NOTOPTERIDAE

Pl. 11

Branchiostegals. Vary from 3–9. *Notopterus* 6–9, *Xenomystus* 3.
Notopterus notopterus and *N. chitla* 8 with none on the epihyal and 8 on the

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[1] Sixteen branchiostegals and an operculum, suboperculum, and interoperculum are reported in the Upper Cretaceous *Enischnorhynchus* by David Bardack, who suggests an elopoid origin for the plethodids (1966. New Upper Cretaceous fish from Texas. U. Kansas Paleont. Contrib., Paper (1): 1–9, 2 fig.).

ceratohyal, 5 external and 3 ventral, all acinaciform in shape; the uppermost large, the others small; branchiostegals 2–5 rest on a small shelf emitted by the upper ceratohyal.

Operculars. In *Notopterus* suboperculum absent. Operculum crenulate; interoperculum entire. Gill membranes united and free from isthmus.

Hyoid arch. In *Notopterus* interhyal (cartilaginous or tendon-like), epihyal, ceratohyal, and one hypohyal (above) present. The lower side of the ceratohyal sends down a wedge-shaped shelf. Branchiostegals 2–5 insert on this shelf. This shelf is probably homologous with that in mormyrids.

References. Boulenger (1904), Day (1875), Hubbs (1920), Khanna (1961), Misra (1953), Munshi (1960), Poll (1957), Ridewood (1905*b*), Weber and de Beaufort (1913).

Material examined. Notopterus notopterus, alizarin specimen, BC55-412, Pakistan.

Suborder Mormyroidei

Superfamily GYMNARCHOIDEA, New Superfamily

Gymnarchidae

Branchiostegals. Four branchiostegals, the upper three on the epihyal and the lower on the ceratohyal. The count of 7 by Hyrtl (*in* Ridewood) is apparently erroneous since all other authors give 4 (he may have had a mormyrid).

Operculars. Complete and entire. The operculum hangs downward from the opercular process of the hyomandibular, instead of swinging out laterally as in other fishes. Suboperculum hidden under the operculum. Gill membranes joined to the isthmus and forming a free fold over it.

Hyoid arch. Epihyal and ceratohyal present. The epihyal is longer and larger than in the Mormyridae. Hypohyals are absent. Ridewood does not mention an interhyal.

Taxonomy. The reorganization of this order and the devaluation of the brain as a systematic character necessitate reduction of the status of this group. The definition of the new superfamily Gymnarchoidea follows Berg's (1947) definition of the suborder Gymnarchoidei.

References. Gregory (1933), Ridewood (1905*b*).

Material examined. None.

Superfamily MORMYROIDEA

Mormyridae

Pl. 11

Branchiostegals. Vary from 6–8 with 4–5 epihyal and 2–3 ceratohyal, usually all on the external face of the hyoid arch. *Mormyrops deliciosa* 7 with 2 free near the epihyal, 3 other on the epihyal, 2 ceratohyal, the anterior 4 virgaform, the upper ones slightly expanded at the ends; *Petrocephalus catostomus* 8 with 4½ epihyal and 3½ ceratohyal, all lateral, uppermost laminar with central ridges, next spathiform, the rest rectilinear acinaciform; *Petrocephalus bane* 8 with 2 free near the epihyal, 2 epihyal, 4 ceratohyal, the anterior 4 on the outer ceratohyal; *Isichthys henryi* 6 virgaform; *Gnatho-*

nemus moori 7 with 4 epihyal and 3 ceratohyal, 6 on the external and 1 on the ventral face of the arch, the branchiostegals resting on a thick flat shelf which projects ventrally from the epihyal and ceratohyal, the uppermost slightly spathiform, the lower ones virgaform.

Operculars. Complete and entire. In *Gnathonemus moori* operculum large, suboperculum reduced to a slender rod, interoperculum a small plate; in *Mormyrops deliciosa* operculum large, suboperculum an elongate triangular plate under the operculum, interoperculum an elongate bone; in *Petrocephalus bane* large operculum covering a small operculum with a small quadrangular interoperculum. Gill openings restricted.

Hyoid arch. In *Mormyrops deliciosa* hypohyals absent, in *Petrocephalus bane* and *P. catostomus* one hypohyal present, an upper one; the other hyoid bones present in all examined; an interhyal is unreported. The interhyal in *Petrocephalus* was tendon-like.

References. Boulenger (1904), Gregory (1933), Ridewood (1905*b*).

Material examined. Isichthys henryi, alcoholic specimen, USNM 114767, Liberia; *Gnathonemus moori*, alcoholic specimen, hyoid arch and branchiostegals alizarin-treated, SU 15699, Cameroons; *Petrocephalus catostomus*, alizarin specimen, NMC63-6645, Angola.

Order **CYPRINIFORMES**

Pl. 11

Branchiostegals 3–20 with 1–3 epihyal and 2–13 ceratohyal, 2–4 external and 1–15 on the ventral (or internal) face of the hyoid arch. Branchiostegals spathiform or at least laminar distally. Gular absent. Opercular bones complete, entire, without spines (except the siluroids which lack the suboperculum). Hypohyals two (but apparently one in Amphiliidae and Chacidae), rest of arch complete. Epihyal and ceratohyal separate or sutured. Gill membranes separate, united to one another and free from or joined to isthmus. Thirty-eight families, all living except one fossil *incertae cedis* family. Known from the Tertiary, questionably from the Cretaceous, to the present.

The presence of up to 20 spathiform branchiostegals, the jaws bordered by premaxillary and maxillary (except in siluroids), the presence of an orbitosphenoid and opisthotic, the absence of true spines, the presence of up to 17 branched caudal rays and up to 17 rays in the abdominal pelvics, the cycloid scales, the usual two hypohyals, and the physostomus gas bladder all indicate that the Cypriniformes belong in the Malacopterygii; together these characters limit derivation from the Clupeiformes.[1] Of the Clupeiformes, the Clupeoidei is the only suborder with the necessary qualifications for an ancestral group. Clupeoid projections on the branchiostegals are shared by both groups. Gosline (1961) states that the caudal skeleton of *Brycon* bears a striking resemblance to that of the round herring, *Dussumieria*. The Dussumieriidae is the only family with a sufficient number of branchiostegals to be ancestral to the Cypriniformes (the Engraulididae also have a sufficient number, but they are precluded as ancestors by their specialized jaws). But the Dussumieriidae may not be immediately ancestral.

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[1] Bertmar (1959) indicates embryological characters of Characidae which he believes are similar to or more primitive than *Amia*. However, rib, scale, hyoid, and caudal skeletal characters would provide strong argument against his interpretation. He later (1961) considered the accessory branchial organs of Characidae to be homologous with those of *Dorosoma* and *Chanos* (both clupeiforms). But (1965) he considers that the characid (*Hepsetus*) pattern of head veins may be primitive and might be the basic type from which the *Acipenser* and *Amia* types evolved and might be close to the ancestral type which gave rise to *Neoceratodus* and *Squalus* (Bertmar, Gunnar, 1965. On the development of the jugular and cerebral veins in fishes. Proc. Zool. Soc. London 144, pt. 1: 87–130, 25 text-fig.). It is difficult to reconcile these (1965) views with other morphological characters.

The Cypriniformes are here divided into two suborders, the Cyprinoidei and the Siluroidei. The Cyprinoidei are characterized by 3–5 usually broad branchiostegals; the presence of parietals, symplectic, suboperculum, and metapterygoid; the parapophyses not co-ossified with the centra; and the epihyals and ceratohyals not sutured. The Siluroidei are characterized by 3–20 slender branchiostegals; the lack of parietals, symplectic, suboperculum, and metapterygoid; the parapophyses co-ossified with the centra; and the epihyals and ceratohyals sutured. From these characters it may be seen that the Cyprinoidei are in general more primitive and less modified than the Siluroidei. Curiously, the branchiostegals have evolved in opposite directions in the two suborders. In the Cyprinoidei they have remained broad and laminar but have become reduced in number, whereas in the Siluroidei the branchiostegals have remained numerous but have become slender in form, expanding only distally into lamina. The suturing of the epihyal and ceratohyal parallels that in the acanthopterygian fishes and follows a general tendency for bones to become sutured in the catfishes (for example, the suturing of the two cleithra to one another).

Suborder Cyprinoidei

Branchiostegals 3–5, at least upper ones spathiform, with 1 epihyal and 2–3 ceratohyal, 2 external and 1–2 ventral or internal. Epihyal, ceratohyal, and hypohyals not sutured. Opercular bones complete. Three superfamilies.

The Cyprinoidea are the most modified of the superfamilies; they have the lower pharyngeal bones enlarged and falciform, unlike the other two families. They doubtless arose from the Characoidea. From the Characoidea also arose the Gymnotoidea which lack dorsal and ventral fins and have an elongate anal fin and an anterior vent. The Characoidea are the most primitive family, since they have the most numerous branchiostegals, normal fins, and the most primitive Weberian apparatus (Alexander, 1962) and other characters (*see* Weitzman, 1962). Regan (1911*b*) revised this group. Weitzman (1962) is followed in uniting the Hemiodontidae, Gasteropelecidae, Citharinidae, Xiphostomatidae, and Anostomidae with the Characidae.[1]

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[1] But within the Characoidei the following families are now recognized by Greenwood, Rosen, Weitzman, and Myers: Characidae, Erythrinidae, Ctenoluciidae, Hepsetidae, Cynodontidae, Lebiasinidae, Parodontidae, Gasteropelecidae, Prochilodontidae, Curimatidae, Anostomidae, Hemiodontidae, Chilodontidae, Distichodontidae, Citharinidae, and Ichthyboridae (1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131: 339–456, 4 pl., 9 text-fig.).

Superfamily CHARACOIDEA

CHARACIDAE (CHARACINIDAE)

Pl. 11

Branchiostegals. Vary from 3–5 with 1 epihyal and 3 ceratohyal, 2 external and 2 ventral, spathiform with clupeoid projections. *Alestes* 4, *Anoptichthys* 3–4, *Anostomus* 4, *Astyanax* 4, *Brycon* 4, *Bryconaethiops* 4, *Carnegiella* 4, *Catroprion* 4, *Citharinus* 4, *Creagrutus* 4, *Cynodon* 5, *Distichodus* 3–4, *Gasteropelecus* 4, *Hemiodus* 4–5, *Hydrocyon* 4, *Ichthyoborus* 4, *Parodon* 4, *Piabucina* 4, *Pseudochalceus* 4, *Sarcodaces* 4, *Tetragonopterus* 4, *Thoracocharax* 5, *Xenocharax* 3, *Xiphostoma* 5. *Astyanax fasciatus* 4 with 1 epihyal and 3 ceratohyal, 2 external and 2 ventral, the anterior 2 fitting into notches in the ceratohyal, all broadly spathiform, the lower three with clupeoid projections. *Brycon meeki* 4 with 1 epihyal and 3 ceratohyal, 2 external and 2 ventral, the anterior 3 with clupeoid projections and all broadly spathiform. *Anostomus anostomus* with 4 spathiform branchiostegals.

Hyoid arch. In *Astyanax* and *Brycon* interhyal, epihyal, ceratohyal, and two hypohyals present.

References. Boulenger (1901), Eigenmann (1917–1929), Gregory (1933), Gregory and Conrad (1938), Günther (1864), Hubbs (1920), Myers (1949), Regan (1911*b*), Schultz (1944), Weitzman (1960, 1960*a*, 1960*b*, 1962).

Material examined. Astyanax fasciatus, alizarin specimen, NMC59-117, Honduras. Alcoholic specimens of the following: *Anostomus anostomus,* BC59-307, Vancouver Public Aquarium; *Anoptichthys jordani,* BC57-62, La Cueva Chica, Pajal, Mexico; *Anoptichthys* sp., BC57-61, Sabinos, Mexico; *Astyanax fasciatus mexicanus,* BC57-417, Gonzales, Mexico.

Superfamily GYMNOTOIDEA

Eigenmann and Allan (1942) are followed in uniting the families Rhamphichthyidae, Sternarchidae, and Electrophoridae (which are recognized by some authors) with the Gymnotidae.

GYMNOTIDAE

Branchiostegals. Four in all genera examined; *Steatogenys, Sternarchus, Gymnotus,* and *Electrophorus. Steatogenys elegans* 4 with the upper 3 broad, the lowest slender. *Gymnotus carapo* 4 broad, rounded, spathiform branchiostegals. *Electrophorus electricus* 4 with 2 external and 2 ventral, the upper two broad and the lower two slender.

References. Ellis (1913), Gregory (1933), Günther (1864), Regan (1911*b*).

Material examined. Steatogenys elegans, alcoholic specimen, BC62-559, aquarium specimen (Guyana?); *Gymnotus carapo,* alcoholic specimen, USNM 179564, Rio Uruba, Brazil; *Electrophorus electricus,* alcoholic specimen, BC58-392, Vancouver Public Aquarium.

Superfamily CYPRINOIDEA

CATOSTOMIDAE

Pl. 11

Branchiostegals. Three spathiform (except sometimes anteriormost is slender) branchiostegals in all examined, with 1 epihyal and 2 ceratohyal, 2 external and 1 internal or ventral. Three found in *Carpiodes, Catostomus, Chasmistes, Cycleptus, Erimyzon, Hypentelium, Ictiobus, Megastomatobus, Minytrema, Moxostoma, Myxocyprinus, Pantosteus, Placopharynx, Thoburnia,* and *Xyrauchen. Catostomus commersonii* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 internal, branchiostegals spathiform with anterior clupeoid projections at base.

Hyoid arch. In *Catostomus* consists of interhyal, epihyal, ceratohyal, and two hypohyals.

Reference. Nelson (1949).

Material examined. Catostomus commersonii, alizarin specimens, NM60-527A & S, Nanticoke, Ontario.

CYPRINIDAE

Branchiostegals. Constantly 3 (although abnormally 4) with 1 epihyal and 2 ceratohyal, and 2 external and 1 internal or ventral. Three branchiostegals found in *Abramis, Alburnus, Aspius, Bliccopsis, Carassius, Cyprinus, Gila, Gobio, Gobiotia, Hampala, Hypothalmichthys, Labeo, Leptobarbus, Leucaspius, Leuciscus, Mylocheilus, Notemigonus, Notropis, Pelecus, Phoxinus, Ptychocheilus, Scardinius, Spirlinus, Tinca, Thynnichthys, Vimba*, and numerous Indian genera (*see* Day). *Cyprinus carpio* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 ventral, spathiform with clupeoid projections on the anterior 2; *Notemigonus crysoleucas* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 ventral, all spathiform and with clupeoid projections on the base; *Gobiotia ichangensis* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 ventral; *Gila* 3 with 1 epihyal and 2 ceratohyal; *Mylocheilus caurinum* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 ventral, all spathiform, only the anteriormost with a clupeoid projection; *Ptychocheilus oregonense* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 internal, all spathiform, the posterior 2 with clupeoid projections; *Notropis bifrenatus* 3 with 1 epihyal and 2 ceratohyal, all spathiform with clupeoid projections. In a sample of 50 specimens of *Richardsonius balteatus* all had 3 branchiostegals.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Cyprinus, Notemigonus, Gila, Hypothalmichthys,* and *Notropis.*

References. Bertin and Arambourg (1958), Boulenger (1901), Chévey (1932), Day (1875), Harrington (1955), Hubbs (1920), Nikolsky (1954), Smitt (1895), Uyeno (1961), Weber and de Beaufort (1916).

Material examined. Cyprinus carpio, skeleton, NMC61-220-S, Rideau Canal, Ontario; *Notemigonus crysoleucas*, alizarin specimen, NMC59-292, Caribou River, Nova Scotia; *Gobiotia ichangensis*, alcoholic specimen, BC53-164, China; *Mylocheilus caurinum*, alizarin specimen, BC54-433, British Columbia; *Ptychocheilus oregonense*, skull, Inst. Fish., University of British Columbia; *Hypothalmichthys moritrix*, alcoholic specimen, BC59-

653, Japan; *Richardsonius balteatus*, 50 alcoholic specimens, BC58-447, British Columbia.

GYRINOCHEILIDAE

Branchiostegals. Gyrinocheilus aymonieri 3 with 0 epihyal and 3 ceratohyal, 2 external and 1 ventral.
References. Bertin and Arambourg (1958), Smith (1945).
Material examined. Gyrinocheilus aymonieri, alcoholic specimen, uncatalogued, University of British Columbia, from Malaya.

COBITIDAE
Pl. 11

Branchiostegals. Constantly 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 ventral. *Cobitis* and *Botia* 3, and 3 in numerous Indian forms (*see* Day, 1875). *Cobitis taenia* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 ventral, slender but expanding into a lamina distally.
Hyoid arch. In *Cobitis* consists of interhyal, epihyal, ceratohyal, and two hypohyals.
References. Day (1875), Smitt (1895), Weber and de Beaufort (1916).
Material examined. Cobitis taenia, alizarin specimen, NMC59-249, Tisa River, Ukraine.

HOMALOPTERIDAE

Branchiostegals. 3 in all forms examined. *Homaloptera zollingeri* 3 spathiform; *Bhavania* 3 with 2 epihyal and 1 ceratohyal; *Hemimyzon abbreviata* 3 with the lowest expanded and spathiform, becoming more slender dorsally.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Bhavania*.
References. Ramaswami (1948), Weber and de Beaufort (1916).
Material examined. Alcoholic specimens of *Hemimyzon abbreviata*, BC53-178, and *Homaloptera zollingeri*, BC58-32, Malaya.

GASTROMYZONIDAE

Branchiostegals. Gastromyzon 3 with 2 on the epihyal and 1 on the ceratohyal.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals.
Reference. Ramaswami (1948).
Material examined. None.

Suborder **Siluroidei**

Branchiostegals 3–20, the distal portion of the upper branchiostegals spathiform with 1–3 epihyal and 2–13 ceratohyal, none or occasionally one on the external face and all or all but one on the ventral or internal face of the hyoid arch, the branchiostegals on the ceratohyal having a forked base; epihyal and ceratohyal usually and ceratohyal and hypohyal often sutured together; operculum and interoperculum present, the interoperculum forked for reception of the operculum; suboperculum absent. The upper branchiostegal characteristically sweeps up into the space vacated by the suboperculum in this suborder. Twenty-eight families.

The most complete revision of the catfishes is still Regan's (1911). There are two main populations of catfishes, the Old World ones (Eurasia and Africa) and the South American ones (also the North American Ictaluridae and the three marine families and derivates, Ariidae, Doiichthyidae, and Plotosidae). The Old World catfishes appear to be more primitive than the South American catfishes, having 4–20 branchiostegals as opposed to 3–17, 6–14 pelvic rays as opposed to (0)5–10(16), and (2)4–8 barbels as opposed to 2–6. The Bagridae and then the Siluridae are the most primitive of the Old World catfishes. The Ictaluridae clearly belong to the Old World catfishes, having 8–13 branchiostegals, 8–9 pelvic rays, and 8 barbels. I agree with Regan that the Ictaluridae are very close to the Bagridae. The Plotosidae are close to the primitive bagrid stock; the Ariidae could be derived from the Bagridae or possibly from the Schilbeidae or Pimelodidae. The Doiichthyidae are apparently derived from the Ariidae (Darlington, 1957).

Of the South American catfishes the Pimelodidae appear to me to be the most primitive. Regan, Berg, and Myers consider the South American Diplomystidae the most primitive of the catfishes; its maxillary is toothed and its 5th vertebra is not suturally connected to the 4th, unlike all other catfishes. However, it is conceivable that the dentition on the maxillary is secondary; other families such as the Chacidae, Pygiidae, and Loricariidae have maxillaries of equal development. The absence of the suture between the 4th and 5th vertebrae may well be secondary rather than primitive. It is notable that the Diplomystidae have relatively few branchiostegals (7–8) and pelvic rays (6) and barbels (2), indicating that the family is rather advanced. The Diplomystidae is therefore considered a moderately advanced family in the suborder and is thought to be derivable from the Pimelodidae or its relatives. The South American freshwater catfishes, according to a survey of 8 characters, are derivable from the Ictaluridae or the Bagridae.

BAGRIDAE (OLYRIDAE)

Branchiostegals. Vary from 6–13. *Macrones* 8–13, *Bagrichthys* 7, *Pseudeutropius* 9–10,[1] *Neotropius* 9,[1] *Bagroides* 7–8, *Leiocassis* 6–11, *Mystus* 9–13, *Rita* 8, *Bagrus* 12, *Chrysichthys* 9, *Clarotes* 9, *Pseudobagrus* 8, *Olyra* 6?, *Liobagrus* 12. *Mystus aor* 11 with 1 epihyal and 10 ceratohyal.

Hyoid arch. In *Rita* and *Neotropius*[1] consists of interhyal, two hypohyals, epihyal, and ceratohyal, the last two sutured together.

References. Day (1875), Günther (1864), Hubbs (1920), Inger and Kong (1962), Jayaram (1953), Khanna (1961), Munshi (1960), Weber and de Beaufort (1913).

Material examined. *Mystus bleekeri*, alcoholic specimen, BC55-402, Thatta, Pakistan; *Liobagrus marginatus*, alcoholic specimen, BC53-168, Szechwan, China.

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[1] *See* footnote under Schilbeidae.

SILURIDAE

Branchiostegals. Vary from 8–20. *Hemisilurus* 10–12, *Ceratoglanis* 10–11, *Belodontichthys* 13–15, *Silurichthys* 9, *Silurus* 12–15, *Wallogo* 15–20, *Hito* 12–14, *Kryptopterus* (= *Cryptopterus*) 8–17. *Silurus glanis* 16 with 3 epihyal and 13 ceratohyal, 1 external and the rest ventral, the uppermost spathiform, the rest acinaciform.

Hyoid arch. In *Silurus* consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal not sutured together, although two prongs from the ceratohyal reach towards the epihyal; similar in *Wallago* but epihyal and ceratohyal are sutured together.

References. Haig (1951), Inger and Kong (1962), Khanna (1961), Smitt (1895), Tomoda (1961), Weber and de Beaufort (1913).

Material examined. Kryptopterus macrocephalus, alcoholic specimen, BC58-32, Malaya; *Silurus glanis,* alizarin specimen, NMC59-290 & S, Ukraine.

SCHILBEIDAE[1]

Branchiostegals. Vary from 7–10. *Helicophagus* 9, *Clupisoma* 8,[1] *Schilbe* 8–10, *Eutropius* 9–10, *Siluranodon* 9, *Schilbichthys* 7, *Lais* 8–9, *Clupisoma garua* 8 with 1 epihyal and 7 ceratohyal.[1]

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Clupisoma.*[1]

References. Günther (1864), Kulkarni (1952), Weber and de Beaufort (1913).

Material examined. None.

CLARIIDAE (SACCOBRANCHIDAE, HETEROPNEUSTIDAE)

Branchiostegals. Vary from 7–15. *Tanganikallabes* 15, *Clariallabes* 9–15, *Gymnallabes* 10, *Channallabes* 8–10, *Dollichallabes* 10, *Vegitglanis* 9, *Horaglanis* 11, *Prophagorus* 10, *Heteropneustes* (*Saccobranchus*) 7–8, *Clarias* 7–9, *Heterobranchus* 7–9.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Heteropneustes.*

References. Gregory (1933), Hubbs (1920), Menon (1951), Weber and de Beaufort (1913).

Material examined. Heteropneustes fossilis, alizarin specimen, NMC62-206-S, India; *Clarias macrocephalus,* alcoholic specimen, BC59-532, Cambodia.

AMBLYCIPITIDAE (AMBLYCEPITIDAE, AKYSIDAE)

Branchiostegals. Acrochordonichthys 6, *Akysis* 6.

References. Günther (1864), Weber and de Beaufort (1913).

Material examined. None.

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[1] Tilak (1964. Proc. Zool. Soc. London 143: 1–36) removes *Pseudeutropius* and *Neotropius* from the Schilbeidae and places them in the Bagridae. He also recognizes the Pangasidae as a distinct family.

CRANOGLANIDIDAE

Branchiostegals. 8 branchiostegals in *Cranoglanis sinensis*.
Relationships. May be close to Bagridae, but closer to Pangasiidae (Myers).
References. Myers (1931), Peters (1880).
Material examined. None.

SISORIDAE[1]

Branchiostegals. Vary from 4–12. *Bagarius* 12, *Glyptosternum* 8–9, *Gagata* 5–7, *Euchiloglanis* 6, *Erethistes* 6, *Sisor* 4. *Euchiloglanis davidi* 6 with 3 epihyal and 3 ceratohyal.
References. Günther (1864), Hora (1942), Weber and de Beaufort (1913).
Material examined. *Euchiloglanis davidi*, alcoholic specimen, BC53-117, Sichang, China.

PANGASIIDAE

Branchiostegals. Vary from 7–11.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal sutured together.
References. Chevey (1932), Günther (1864), Inger and Kong (1962), Khanna (1961), Weber and de Beaufort (1913).
Material examined. None.

AMPHILIIDAE

Branchiostegals. 9 in *Amphiluus grandis*, the upper two slightly expanded distally. *A. platychir* 9 with 2 epihyal and 7 ceratohyal, 4 posterior on the ventral and 5 anterior on the internal face of the hyoid arch, all acinaciform.
Hyoid arch. Consists of interhyal, epihyal which is sutured to the ceratohyal, and one hypohyal (the two hypohyals apparently fused).
Reference. Günther (1864).
Material examined. *Amphiluus grandis*, alcoholic specimen, USNM 72922, Nairobi River, Africa; *A. platychir*, alizarin specimen, NMC63-67 & S, Northern Rhodesia.

MOCHOCIDAE (SYNODONTIDAE)

Branchiostegals. Vary from 5–7. *Mochocus* 5, *Synodontis* 6–7. *Mochocus niloticus* upper two expanded distally. *Synodontis woosnami* 7 with 2½ epihyal and 4½ ceratohyal, 3 external and 4 internal, all acinaciform.
Hyoid arch. Consists of interhyal, epihyal which is sutured to the ceratohyal, and two hypohyals.
References. Boulenger (1911), Günther (1864), Regan (1911).
Material examined. *Mochocus niloticus*, alcoholic specimen, USNM 61297, Egypt; *Synodontis woosnami*, alizarin specimen, NMC63-68 & S, Northern Rhodesia.

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[1] A count of 6, with 3 epihyal and 3 ceratohyal, 3 lateral and 3 ventral, with both the epihyal and ceratohyal, and the ceratohyal and hypohyal suturally united, and with the interhyal absent, was reported by C.L. Mahajan (1966. *Sisor rabdophorus*—A study in adaption and natural relationships. I. The head skeleton. J. Zool. London 149: 365–393, 2 fig.).

MALAPTERURIDAE

Branchiostegals. 6 in *Malapterurus electricus*, the upper two stout and curved.
Reference. Günther (1864).
Material examined. Malapterurus electricus, alcoholic specimen, USNM 118779, Liberia.

CHACIDAE

Pl. 11

Branchiostegals. 8 in *Chaca chaca* with 2 on the epihyal and 6 on the ceratohyal, all on the ventral face of the arch, the upper two stout. (But according to Weber and de Beaufort only 6 branchiostegals.)
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and apparently only one hypohyal (or two hypohyals very closely sutured). Epihyal and ceratohyal sutured together. Posterior ventral surface of ceratohyal flattened.
References. Günther (1864), Weber and de Beaufort (1913).
Material examined. Chaca chaca, alizarin specimen, NMC62-205 & S, India.

PLOTOSIDAE

Branchiostegals. Vary from 7–13. *Paraplotosus* 9–11, *Plotosus* 11–13, *Cnidoglanis* 7, *Oloplotosus* 10 or 12 (?), *Porochilus* 7, *Copidoglanis* 8–10. *Plotosus anguillaris* 11 with 1 epihyal and 10 ceratohyal, all on the ventral surface of the arch, the upper 2 spathiform distally.
Hyoid arch. In *Plotosus* consists of interhyal, epihyal, ceratohyal, and two hypohyals, the three latter sutured together.
References. Günther (1864), Weber and de Beaufort (1913).
Material examined. Plotosus anguillaris, alizarin specimen, NMC62-204 & S, India.

ARIIDAE

Branchiostegals. Vary from 5–9 (12) with 1–1½ epihyal and 4–4½ ceratohyal, all ventral. *Arius* 5–7 (8–9), *Ketengus* 5, *Tetranesodon* 6, *Nedystoma* 6, *Hemipimelodus* 5–8 (12), *Osteogeneiosus* 5, *Batracocephalus* 5, *Cathorops* 6, *Aelurichthys* 6. *Galeichthys felis* 5 with 1 epihyal and 4 ceratohyal, all ventral, the upper two spathiform, the lower acinaciform. *Cathorops gulosa* 6 with 1½ epihyal and 4½ ceratohyal.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and 2 hypohyals in *Galeichthys* and *Cathorops*, all but the interhyal being sutured together.
References. Chevey (1932), Day (1875), Günther (1864), Hubbs (1920), Weber and de Beaufort (1913).
Material examined. Galeichthys felis, alizarin specimen, NMC62-74 & S, North Carolina; *Cathorops gulosa*, alizarin preparation, BC59-670, Panama.

DOIICHTHYIDAE

Branchiostegals. Doiichthys novaeguineae 6.
Reference. Weber and de Beaufort (1913).
Material examined. None.

ICTALURIDAE

Branchiostegals. Vary from 8–13 with 2 epihyal and 7–8 ceratohyal, all ventral. *Pylodictis* 12–13, *Noturus* 9, *Satan* 10–11, *Trogloglanis* 9, *Prietella* 9, *Ictalurus* 8–9. *Ictalurus nebulosus* 2 epihyal and 7 ceratohyal, all ventral, upper two spathiform, rest acinaciform.

Hyoid arch. Interhyal, epihyal, ceratohyal, and two hypohyals present. Epihyal, ceratohyal, and hypohyals sutured together.

References. Hubbs (1920), Jordan and Evermann (1896), Suttkus (1961), Taylor (1955).

Material examined. Ictalurus nebulosus, skeletal specimen, NMC61-218-S, Ottawa, Ont.; *I. nebulosus*, alizarin specimen, BC59-601, Dewdney Slough, B.C.; *I. nebulosus*, alizarin specimen, NMC61-528-A, 3 miles west of Selkirk, Ont.; *I. punctatus*, skeletal specimen, NMC61-217-S, Ottawa, Ont.; *Noturus gyrinus*, alcoholic specimen, BC55-482, Virginia.

DIPLOMYSTIDAE

Branchiostegals. Diplomystes 8.

References. Eigenmann and Eigenmann (1890), Günther (1864).

Material examined. None.

DORADIDAE (AUCHENIPTERIDAE)

Branchiostegals. Vary from 6–7. *Auchenipterus* 6–7, *Trachelyopterus* 6, *Doras* 7.

References. Eigenmann (1925), Günther (1864).

Material examined. None.

AGENIOSIDAE

Branchiostegals. Ageniosus 11.

Reference. Günther (1864).

Material examined. None.

PIMELODIDAE

Branchiostegals. Vary from 6–17. *Pseudoplatystoma* 14–15, *Sorubim* 15–16, *Platystoma* 11–17, *Hemisorubim* 10–11, *Platystomichthys* 9, *Sciades* 9, *Pimelodus* 6–9, *Callophysus* 7–8, *Heptapterus* 8–9, *Rhambdia* 6. *Rhambdia guatemalensis* 6 with 1 epihyal and 5 ceratohyal, all ventral, upper two expanded.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Rhambdia*; not sutured together.

References. Eigenmann and Allan (1942), Günther (1864), Regan (1911*c*).

Material examined. Rhambdia guatemalensis, alizarin specimen, NMC62-708-S, Yucatan.

HELOGENIDAE

Branchiostegals. Helogenes marmoratus 13.

References. Günther (1864), Regan (1911*c*).

Material examined. None.

HYPOPHTHALMIDAE

Branchiostegals. Hypophthalmus 13–15, long slender virgaform.
References. Günther (1864), Regan (1911*c*).
Material examined. Hypophthalmus edentatus, alcoholic specimen, USNM 86285, Peru.

CETOPSIDAE

Branchiostegals. Cetopsis 8.
References. Günther (1864), Regan (1911*c*).
Material examined. None

PYGIIDAE (TRICHOMYCTERIDAE)

Branchiostegals. Vary from 7–8 (12). *Nematogenys* 12, *Pygidium* (= *Trichomycterus, Thrycomycterus*) 7–8, *Eremophilus* 8. *Pygidium punctulatus* third branchiostegal expanded distally.
Operculars. Family, except *Nematogenys*, characterized by presence of several prickles on the operculum and interoperculum.
Relationships. Nematogenys differs from other genera in that it has more numerous branchiostegals and in that it lacks prickles on the operculars, and so on. Eigenmann (1918) awarded it subfamilial recognition and considered it more primitive than the other genera, but in 1926 (reference not seen) he raised it to familial level. The latter position is more in accord with the numerous branchiostegals. Alternatively it might be possible that the genus belongs in some other family. The opercular spines are used for working forward into small openings under rocks and for climbing waterfalls and may also function in branchial parasitism.
References. Eigenmann (1918), Ferreira and Soriano (1960), Günther (1864), Regan (1911*c*).
Material examined. Pygidium punctulatus, alcoholic specimen, USNM 88674, Peru.

ASPREDINIDAE (BUNOCEPHALIDAE)

Branchiostegals. 5 in *Bunocephalus* and *Aspredo.*
Taxonomy. Myers (1960*a*) is followed in uniting the Bunocephalidae with the Aspredinidae.
References. Günther (1864), Myers (1960*a*), Regan (1911*c*).
Material examined. None.

CALLICHTHYIDAE

Branchiostegals. Vary from 3–4. *Hoplosternum* 3, *Callichthys* 4, *Corydoras* 3. *Corydoras aeneus* 3 with 1 epihyal and 2 ceratohyal, all ventral, upper one spathiform.
Hyoid arch. In *Corydoras* consists of interhyal, epihyal, ceratohyal, and two hypohyals. Hyoid bones not ankylosed together. Top of ceratohyal flattened; in lateral view ceratohyal broad posteriorly, narrowing anteriorly.
Reference. Günther (1864).

Material examined. Corydoras aeneus, alizarin specimen, NMC62-134-S, aquarium specimen; *Hoplosternum littorale*, alcoholic specimen, BC59-307, aquarium specimen.

LORICARIIDAE

Branchiostegals. Regan gives the number of branchiostegals as 4 in the family description.
Operculars. Prickles may be present on the interoperculum and operculum of certain members of the Plecostominae.
References. Günther (1864), Jordan and Evermann (1896), Regan (1904).
Material examined. None.

ASTROBLEPIDAE (ARGIIDAE)

Branchiostegals. Astroblepus (= *Arges, Stygogenes*) 4.
Operculars. Gill membranes joined to isthmus. Said to take water in through an orifice at the top of the gill opening. Since *Astroblepus* has sucker-like lips, this method of inhaling water is doubtless an adaption similar to that in the Gyrinocheilidae.
References. Gosline (1947), Günther (1864).
Material examined. None.

Order ANGUILLIFORMES

Pl. 11

Branchiostegals 6–22 with 4–12 epihyal and 0–4 ceratohyal, all on the external face of the hyoid arch, usually filiform or virgaform, occasionally upper ones expanded distally, curving up around behind and often to above the upper border of the gill cover; jugostegelia sometimes present; gular absent; opercular bones usually complete, lacking spines, and entire or rarely crenulate (but interoperculum absent in Moringuidae and suboperculum and interoperculum absent in some Nemichthyidae). Suboperculum usually crescentic, curving up around behind operculum; operculum usually shaped like a short-handled spoon and curved downwards; gill membranes joined to isthmus, opening restricted; interhyal absent (in adults) and sometimes the single hypohyal absent. Epihyal and ceratohyal present (not sutured but may overlap), usually slender, the epihyal forked at the dorsal tip, the epihyal and posterior ceratohyal not greatly expanded. Upper Cretaceous to present. Twenty-five families of which three are known only from fossils.

This order is well characterized by the peculiarities of the branchiostegal series, by the spoon-shaped operculum bordered posteriorly and often dorsally by the curved suboperculum, and by the slender upcurled branchiostegals. These striking characters enable recognition of a fossil anguilliform misplaced amongst the Halosauridae. There is little doubt that all forms investigated belong to the Anguilliformes and that it is a monophyletic group. Regan (1912*b*) and Trewavas (1932) are the main studies on this group. Gosline (1952) reports on four families, and Asano (1962) reviews the Japanese Congridae.

The peculiarities of the branchiostegal series are doubtless related to the pharyngeal-type respiration, the expanded gill cavity, and the reduced gill opening. With the adherence of the gill membranes to the isthmus, the hyoid arch pivots little, if at all, with gill cover movements. This restriction of pivotal movement may be related to the loss of the interhyal. Similarly, the hypohyals at the bottom of the arch are reduced to one or are absent, and the epihyal and ceratohyal become very slender. (However the epihyal and ceratohyal are still stout in the fossil families.) The branchiostegals no longer impel the gill membrane (unlike most fishes) and become reduced to reinforcing rods. The branchiostegal membrane here forms a muscular pulsing wall along which peristaltic waves pass which draw water through the gills and out the gill opening. The mouth need not close during this process.

The origin of the eels is not yet settled. Woodward (1901) held that they were derived from the ganoids. Regan (1912*b*) concluded that they must be descended from clupeoid fishes. Gregory (1933) thought it not impossible that the eels might stand as a specialized offshoot from near the base of the Iniomi.

The fact that the maxillary enters the gape, together with the physostomus gas bladder, indicates that the eels were derived from the Clupeiformes or Leptolepiformes rather than from the Myctophiformes. The leptocephalus larvae and the absence of ganoine in the eels would be in agreement with clupeiform derivation.

However, the resemblance of the suboperculum and branchiostegals between the Anguilliformes and the Myctophoidei (in both, the suboperculum and branchiostegals curve around the operculum and the branchiostegals are long, slender, and curved) does offer some support to the hypothesis of anguilliform derivation from the myctophiforms. The anguillavid *Enchelurus syriacus* is not unlike the synodontids. A solution to these alternatives is derivation from an elopoid line which was also ancestral to the myctophiforms. The single hypohyal might indicate a leptolepiform ancestry.

Eel classification is in a confused state, only partly because of the absence of knowledge of structures for classifying the different groups. A fairly sound basic framework of internal morphology exists. But many eels have been classified purely on the basis of external appearance and hence may have been misplaced.

The branchiostegal series and related bones offer several characters to assist in the classification of the eels. Among these are the number of branchiostegals, whether the upper branchiostegal is expanded into a crescent, the arrangement of the branchiostegals on the hyoid bones, whether the branchiostegal base projects beyond the hyoid arch, the shape of the suboperculum (wedge-shaped or arc-shaped), the presence of the interoperculum, the fusion of the hyoid bones (some authors may have missed the unusual diagonal overlap of the epihyal and ceratohyal found in at least some of the eels), and the presence of a hypohyal. The upper bone of the hyoid arch appears to be the epihyal; the lower ceratohyal and a hypohyal may be present in some. The author has not discovered a bone definitely identifiable as an interhyal in adult eels. But an interhyal is known in larvae of *Anguilla* (de Beer, 1937) and of *Serrivomer* (Bauchot, 1959).

The living eels are generally divided into three groups: the anguillid, the congrid, and the nemichthyid. The first two are distinguished by whether the frontal bones are ankylosed or united by suture. A further group may be distinguished within the congrid-type eels, those families in which certain branchiostegals are free from the arch, overlapping on the midventral line, and in which the branchiostegals are more numerous (17–51 as opposed to 22 or fewer). Branchiostegals free from the arch are known in Echelidae, in Ophichthidae, and apparently in Neenchelidae. They were termed jugostegelia by Parr (1930), who believed that they were not homologous with branchiostegals. But the fact that some branchiostegals in other families may be free from the arch (e.g., a free branchiostegal occurs in *Nessorhamphus* and 6 in *Gymnothorax*) together with the close morphological similarity of jugostegelia and branchiostegals leads one to believe they are homologous. Nevertheless it is useful to retain the term for those secondarily multiplied, overlapping and free branchiostegals found in certain anguilliforms. The jugostegelia probably function in supporting the walls of an elongated branchial cavity.

†ANGUILLAVIDAE

Branchiostegals. Anguillavis quadripinnis at least 12; *A. bathshebae* at least 15 slender virgaform branchiostegals, some of the upper ones broadening out and curling upwards at their distal ends. In *Enchelurus syriacus* at least 8 slender branchiostegals which curl up behind the suboperculum.

Operculars. The opercular bones appear to resemble those of *Anguilla*, but only impressions remain. In *Enchelurus syriacus* the suboperculum is a narrow band which parallels the operculum ventrally and posteriorly.

Hyoid arch. Relatively stout and well developed; at least epihyal and ceratohyal present.

Relationships. The genus *Enchelurus* has been placed in the Halosauridae by Woodward (1901) and Romer (1955), probably because of the presence of pelvic fins which are absent in living eels. However, several characteristics strongly suggest that *Enchelurus* belongs amongst the primitive anguilliforms: the high number of vertebrae (about 100), the reduced caudal skeleton, the narrow pectoral girdle separated from the skull, the suboperculum and interoperculum curling around behind the operculum, the slender virgaform branchiostegals, the presence of an orbitosphenoid, the laminar anterior neural arches. Neither the terminal mouth, the suboperculum, nor the branchiostegals agree with the Halosauridae. The presence of pelvic fins indicates that *Enchelurus* should be placed in the Anguillavidae

A further comment may be made on Woodward (1901). His material of *Enchelurus syriacus* appears to be composed of two species. The holotype (P5998) has at most 20 dorsal rays, whereas a second specimen (P9168) appears to have at least 52 rays. The latter specimen and *E. anglicus* appear to be closer to *Anguillavis* in the length of their dorsals. *E. syriacus* (P5998) would appear to be the most primitive of eels judging by its short dorsal fin. It is possible, contrary to Regan, that *Anguillavis quadripinnis* is not a dercetid. The shortness of its dorsal does not remove it from the eels since *Enchelurus* may have an even shorter dorsal, and the rows of bony lateral plates might be the normal lateral line scales found in anguilliforms.

References. Hay (1903), Regan (1912*b*), Romer (1955), Woodward (1901).
Material examined. None.

†URENCHELYIDAE

Branchiostegals. In *Urenchelys* about 11 slender branchiostegals; these tend to curve up around the operculum.
References. Hay (1903), Woodward (1901).
Material examined. None.

†MYLOMYRIDAE

Branchiostegals. Only four branchiostegals remain in the specimen; some are probably missing. Branchiostegals slender and virgaform.
Reference. Woodward (1910).
Material examined. None.

ANGUILLIDAE

Branchiostegals. Vary from (8) 9–12 (13, 14). *Anguilla rostrata* 11 with 9 on the epihyal and 2 on the ceratohyal, all on the external face, all filiform and curving up around to the posterodorsal corner of the operculum. The upper portion of the uppermost branchiostegal expanded and scythe-like. Branchiostegals of two sides do not overlap.
Hyoid arch. Interhyal and hypohyal absent. Ceratohyal sends a prong over the dorsal edge of the epihyal; there is a short gap between their lower edges.
References. Day (1875), Ege (1939), Smitt (1895).
Material examined. Anguilla rostrata, alizarin specimen, NMC60-221, Magdalen Islands, Quebec.

MURAENIDAE
Pl. 11

Branchiostegals. 9 in *Muraena lentiginosa* and *Gymnothorax dovii.* In the latter, the lower 3 branchiostegals insert on the epihyal, the rest are free. In *Muraena lentiginosa* the branchiostegals turn around parallel with or past the upper end of the epihyal; none insert upon the arch. Branchiostegals slender and filiform, curving up around behind to above the posterodorsal edge of operculum; those of the two sides do not overlap.
Hyoid arch. Consists of very narrow epihyal and ceratohyal. Epihyal angulated and slightly forked at its dorsal end.
References. Gregory (1933), Regan (1912*b*).
Material examined. Muraena lentiginosa, alizarin specimen, BC59-241, Las Tres Marias, Mexico; *Gymnothorax dovii*, alizarin specimen, NMC59-141, Maria Magdalena Island, Las Tres Marias Islands, Mexico.

MYROCONGRIDAE

Branchiostegals. No data available.
Relationships. Apparently only one specimen known. According to Regan it

is as closely related to the Anguillidae as to the Muraenidae.
References. Günther (1870), Regan (1912*b*).
Material examined. None.

XENOCONGRIDAE (CHLOPSIDAE, CHILORHINIDAE)

Branchiostegals. Vary from 12–21. *Kaupichthys* 14–15, *Chilorhinus* 15–21, *Chlopsis* 12. *Kaupichthys diodontus* 15 and, according to the figure, all on the epihyal (labelled as ceratohyal). *Chilorhinus suensoni* 15–21, usually 17–19. Branchiostegals slender and circling around to posterodorsal corner of operculum. Rays of two sides do not overlap.
Hyoid arch. Consists of long angulate epihyal and short ceratohyal in *Kaupichthys*; in *Chilorhinus* ceratohyal and epihyal short and stout.
References. Böhlke (1956), Garman (1899), Gosline (1950, 1951, 1952).
Material examined. None.

DYSOMMINIDAE

Branchiostegals. *Dysommina rugosa* about 16.
Relationships. According to Böhlke and Hubbs close to Heterenchelidae. Moringuidae, and Xenocongridae.
References. Böhlke and Hubbs (1951).
Material examined. None.

HETERENCHELIDAE

Branchiostegals. In *Heterenchelys microphthalmus* 14 long slender branchiostegals, none expanded. Curve up around behind operculum to its posterodorsal border; those of the two sides do not overlap.
Reference. Regan (1912*b*).
Material examined. None.

MORINGUIDAE (ANGUILLICHTHYIDAE)

Branchiostegals. In *Stilbiscus bahamensis* 10 slender branchiostegals which curve up behind the operculum, the uppermost expanded distally with posterior border crenulate. From Trewavas's figure, apparently 4 on the epihyal and 6 on the long ceratohyal. Those of the two sides do not overlap. *Moringua macrochir* 9 filiform branchiostegals.
Hyoid arch. Epihyal apparently shorter than the ceratohyal; hypohyal absent.
References. Gosline and Strasburg (1956), Trewavas (1932).
Material examined. *Moringua macrochir*, alizarin specimen, NMC63-120-S, Hawaii.

SYNAPHOBRANCHIDAE

Branchiostegals. Vary from 13–19. In *Synaphobranchus* 13–15 attached to the external face of the epihyal and ceratohyal and (contrary to Gill) curving up behind the opercular bones. In *Diastobranchus capensis* 18–19 slender, curving up around the opercular bones, the upper four being expanded distally. Those of the two sides do not overlap.

Hyoid arch. Epihyal and ceratohyal present.
References. Castle (1961), Gill (1891), Jordan and Evermann (1896).
Material examined. None.

ILYOPHIDAE

Branchiostegals. Ilyophis brunneus 14–15, non-overlapping, sweeping up around the operculars, the upper expanded.
References. Gilbert (1891), Jordan and Evermann (1898).
Material examined. Ilyophis brunneus, alcoholic specimen, USNM 185665, Florida.

SIMENCHELYIDAE

Branchiostegals. 8–10 in *Simenchelys parasiticus*, slender, elongate, curving up around operculars. Distal extremities of upper 4–5 expanded.
Relationships. The expansion of the upper branchiostegals and the ventral gill slits would appear to relate it to the Synaphobranchidae, and Ilyophidae. Gosline (1952) has indicated that the Simenchelyidae belong in the group with ankylosed frontals.
References. Castle (1961), Gill (1891*b*), Gosline (1952).
Material examined. None.

CONGRIDAE

Branchiostegals. Vary from 8–17 with 5–8 epihyal and 1–4 ceratohyal, all external. *Taeniconger* 10, *Nystactichthys* 7, *Gorgasia* 8, *Conger* 8–10, *Uroconger* 9–17, *Chiloconger* 9, *Congrosoma* 13, *Xenomystax* 11–12, *Ariosoma* 8–17, *Xenoconger* 11 or 12, *Anago* 9, *Alloconger* 9–11, *Congriscus* 9, *Rhynochocymba* 8–9, *Rhynchoconger* 8, *Promyllantor* 9, *Japonoconger* 9, *Congrina* 8. *Conger myriaster* 9 with 5 epihyal and 4 ceratohyal, all external, upper three slightly broader. *Taeniconger* sp. 10 with 8 epihyal and 2 ceratohyal, all external, upper two expanded distally, remainder filiform. *Gorgasia punctata* 8 with 7 epihyal and 1 ceratohyal, all external; the two tips of the medial branchiostegals of each side meet but do not overlap; branchiostegals curve up around behind operculum. *Ariosoma prorigera* 12 that curve up around dorsal edge of operculum. *Nystactichthys* 7 with 5 epihyal and 2 ceratohyal. In none examined do the branchiostegals of the two sides overlap.
Hyoid arch. In *Taeniconger* consists of a ceratohyal, which sends a dorsal prong over the epihyal, and a triangular hypohyal; all bones stout. In *Conger* the stout ceratohyal sends a dorsal prong over the epihyal. In *Nystactichthys* consists of epihyal, ceratohyal, and hypohyal.
References. Asano (1962), Böhlke (1957, 1958), Day (1875), Garman (1899), Gilbert (1891), Gosline (1952), Jordan and Evermann (1896), Myers and Wade (1941), Regan (1912*b*), Smitt (1895), Trewavas (1932).
Material examined. Taeniconger sp., alizarin specimen, NMC62-226-S, Ceralbo Island, Mexico; *Ariosoma prorigera*, alcoholic specimen, BC61-169, Mazatlan, Mexico; *Gorgasia punctata*, alizarin specimen, NMC62-211 & S, Petacalco Bay, Guerrero, Mexico.

MURAENESOCIDAE

Branchiostegals. Vary from 8–22. *Muraenesox* 16–22, *Hoplunnis* 8. *Muraenesox coniceps* 16 virgaform which curve up around operculum; *Hoplunnis* sp. 8 virgaform which curve up behind the operculars, the upper branchiostegals being expanded. Those of the two sides do not overlap.

Relationships. The disparity in branchiostegal count between the two genera is noteworthy.

References. Day (1875), Regan (1912*b*), Trewavas (1932).

Material examined. Hoplunnis sp., alcoholic dissected specimen, BC61-169, Mazatlan, Mexico. *Muraenesox coniceps*, alcoholic dissected specimen, BC59-665, off Rio Pasigo, Panama.

DERICHTHIDAE

Branchiostegals. 7 in *Derichthys serpentinus*, all arising from the external face of the fused epihyal-ceratohyal, with swollen bases, slender and curving up behind the operculars; upper ones not expanded. Those of the two sides do not overlap.

Hyoid arch. A single stout element formed by fusion of the epihyal and ceratohyal.

Taxonomy. Note removal of *Gorgasia* and *Benthenchelys* to the Congridae.

References. Beebe (1935), Gosline (1952), Trewavas (1932).

Material examined. None.

NESSORHAMPHIDAE

Branchiostegals. 6–7 slender filiform branchiostegals in *Nessorhamphus ingolfianus*. These curve up around to above the middle of the operculum. The upper and lowest fail to insert on the hyoid arch in Trewavas's specimen, failing slightly short of it, but in Beebe's specimen the lowest does reach the arch. The epihyal and ceratohyal are fused; a hint of the fusion point indicates one branchiostegal on what would be the ceratohyal portion, the remainder on the epihyal portion. Those of the two sides do not overlap.

Hyoid arch. Epihyal and ceratohyal fuse to form a single bone; a trace of separation in one specimen between the anteriormost and adjacent branchiostegals.

References. Beebe (1935), Trewavas (1932).

Material examined. None.

NETTASTOMIDAE

Branchiostegals. 7 branchiostegals in *Nettastoma* sp., slender, curving up around operculum to its dorsoposterior corner. Those of the two sides do not overlap.

Reference. Goode and Bean (1896).

Material examined. Nettastoma sp., alcoholic specimen, USNM 157939, from south of Great Bahamas Island.

NEENCHELIDAE[1]

Branchiostegals. Neenchelys 25 filiform branchiostegals which curve up around operculum. Only 5 insert on the hyoid arch (*ergo* 5 branchiostegals +20 jugostegelia). Those of the two sides apparently overlap.
References. Bertin and Arambourg (1958), Weber and de Beaufort (1916).
Material examined. None.

OPHICHTHIDAE (ECHELIDAE, MACROCEPHENCHELYIDAE)

Branchiostegals. Vary from 17–51, filiform (including 4–46 jugostegelia), which overlap those of the other side. *Brachysomophis* 18, *Caecula* 17, *Chlevastes* 25, *Cirrhimuraena* 24, *Cryptopterenchelys* 22, *Leiuranus* 28, *Myrichthys* 32, *Myrophis* 41–51, *Muraenichthys* 26–30, *Phyllophichthys* numerous overlapping, *Pisodonophis* 29–31. *Myrichthys* 28 plus 4 jugostegelia which lie slightly behind the arch. *Myrophis* 5 plus 36–46 jugostegelia which overlap. *Leptenchelys* described as having overlapping jugostegelia. *Muraenichthys cookei* 6 plus 24 jugostegelia which overlap those of the opposite side.
Hyoid arch. Epihyal and ceratohyal fused (according to fig. *in* Gosline, 1951).
Taxonomy. Gosline (1952) is followed in uniting Echelidae with Ophichthidae.
References. Day (1875), Garman (1899), Gosline (1951, 1952), Myers and Wade (1941), Parr (1930).
Material examined. Muraenichthys cookei, alizarin specimen, NMC63-120-S, Hawaii.

DYSOMMIDAE

Branchiostegals. None externally apparent in thick skin—no data available.
Relationships. Bertin and Arambourg (1958) lump this family with Ilyophidae.
References. Alcock (1889), Barnard (1927), Böhlke (1949), Matsubara (1936), Tomiyama and Abe (1958), Trewavas (1932).
Material examined. None.

SERRIVOMERIDAE

Branchiostegals. Vary from 7–8 with 6–7 epihyal and 1 ceratohyal, elongate slender branchiostegals with bases broadened and ends curling up around to postero-dorsal corner of operculum. *Serrivomer samoensis* 7 with 6 epihyal and 1 ceratohyal, the 3 central rays with broadened bases and tips extending beyond hyoid arch. *Serrivomer brevidentatus* 8 with 7 epihyal and 1 ceratohyal, only the second and third with tips extending beyond the hyoid arch, the rest inserting on the external face of the arch. *Serrivomer sector* 7 with 6 epihyal and 1 ceratohyal, only the tip of the third branchiostegal projecting beyond the arch, the upper two without flattened bases, all but the third inserting on the external face of the arch. *Platuronides danae* and *P. acutus* 8 with 7 epihyal and 1 ceratohyal, the tips of the second and third extending beyond the hyoid arch. The body of the branchiostegals is filiform, the tips tend to curve up around the operculum, and the branchiostegals of the two sides fail to overlap in all species examined.

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[1] Gareth J. Nelson reports 30 or more branchiostegals in *Neenchelys*, 6 of which are articulate with the ceratohyal, the rest being free and overlapping mid-ventrally. He refers the Neenchelidae to the Echelinae, family Ophichthidae (1966. Osteology and relationships of the eel, *Neenchelys buitendijki*. Copeia (2): 321–324, 2 fig.).

Hyoid arch. In adult *Serrivomer* and *Platuronides* a fairly stout ceratohyal and angulated epihyal present; interhyal and hypohyals unknown. Bauchot (1959) indicates an interhyal in larval *Serrivomer* and a single cartilage, the precursor of the epihyal and ceratohyal. Lack a ceratohyal prong extending over the dorsal side of the epihyal.

References. Bauchot (1959), Beebe (1935), Beebe and Crane (1936, 1937), Castle (1961), Garman (1899), Trewavas (1932).

Material examined. Serrivomer sector, alcoholic specimen, BC62-163, Guadalupe Island, Mexico.

NEMICHTHYIDAE (AVOCETTINIDAE)

Branchiostegals. Vary from 7–15 with 7–12 on the epihyal and 0 on the ceratohyal, all inserting on the external face of the hyoid arch, sometimes the tips of the rays extending beyond the arch. *Nemichthys* 8–15, *Avocettina* 7–12, *Labichthys* 8–9, *Nematoprora* 9. *Avocettina gilli* 7 with 7 epihyal and 0 ceratohyal, all filiform and external and curving around in an arc up behind the operculum. *Labichthys carinatus* 8 with 8 on the external face of the epihyal and 0 on the ceratohyal, the lower ones with the bases extending beyond the arch. *Avocettina* sp. 12 with 12 epihyal and 0 ceratohyal, all inserting on the external face of the arch.

Hyoid arch. Epihyal and ceratohyal present in *Avocettina* and *Labichthys.*

Relationships. Nemichthyidae lack a branchiostegal on the ceratohyal, unlike the Serrivomeridae.

References. Beebe and Crane (1937*a*), Berg (1947), Bertin and Arambourg (1958), Castle (1961), Garman (1899), Trewavas (1932).

Material examined. Nemichthys scolopaceus, alcoholic specimen, BC62-162, off Point Loma, California.

CYEMIDAE

Branchiostegals. Absent.

References. Berg (1947), Bertin and Arambourg (1958).

Material examined. None.

AVOCETTINOPSIDAE

Branchiostegals. 8–10 in *Avocettinops*, all on the external face of the epihyal, the bases of the lower two projecting over to the other side, slender and curved upwards. A pair of long slender elements, one on either side of the midline commencing opposite the anterior end of the ceratohyal, may represent branchiostegals, but more likely they are parts of a split urohyal (partially split in *Avocettina*).

Hyoid arch. Consists of epihyal, ceratohyal, and hypohyal (these equal, respectively, ceratohyal, hypohyal, and glossohyal of Bertin and Arambourg). Epihyal and ceratohyal non-overlapping.

References. Bertin and Arambourg (1958), Böhlke and Cliffe (1956), Norman (1939).
Material examined. None.

Order GIGANTURIFORMES

Branchiostegals, gulars, interhyal, epihyal, ceratohyal, and hypohyals absent. Opercular bones complete and entire, without spines. Suboperculum larger than operculum. Gill openings restricted. A single family in recent oceans.

Relationships. Regan (1925) derived the giganturids from the synodontids and considered that they may have been a specialized offshoot from a line that led to the Lyomeri. Fowler (1936) considered *Stylephorus* and *Gigantura* to be related. Walters (1961) came to a conclusion similar to Regan's, that the Giganturoidea may be a specialized offshoot of a line that led from a submyctophiform group, such as the esocoids, towards the synodontoid myctophiforms and that this line later may have given rise to the Cetunculi and perhaps eventually to the Lyomeri. He considered *Stylephorus* and *Gigantura* unrelated.

In a comparison of about 30 morphological characters in the lower orders, the Giganturidae were found closest to the Notacanthiformes, Saccopharyngiformes, and Anguilliformes, and of these three, especially the Saccopharyngiformes, closest to the Anguilliformes. However, the similarities between these groups are mainly based on the absence of characters, an unsound method of basing phylogeny. It is unlikely that the Anguilliformes were ancestral to the Giganturiformes, although they may have had a common ancestor.

The hyoid arch is much reduced in the Saccopharyngiformes (Orton, 1963) and essentially absent in the Giganturiformes. Further, the Saccopharyngiformes agree with the Giganturiformes in more characters than any other order. When compared to the Saccopharyngiformes, the Giganturiformes are more primitive and less degenerate in that they possess opercular bones, a developed caudal fin, and a more normal body and fin arrangement. I agree, therefore, with the possibility that the same stock that gave rise to the Giganturiformes might have given rise to the Saccopharyngiformes.

In conclusion, one can only say that the great degeneration that has taken place in the Giganturidae makes it difficult to judge its derivation. But that it is a soft-rayed fish and that it will be traced eventually to either the Clupeiformes or the Myctophiformes seems most plausible. It is unfortunate that the caudal osteology is as yet undescribed. Judging from the fairly numerous caudal rays, the caudal skeleton cannot be too reduced and might well hold the secret of the giganturids' progenitors. The same holds for the axial skeleton.

The opercular bones are peculiar. The heavy down-bent operculum with its posterior suboperculum resembles the operculum of Anguilliformes and of Synbranchiformes. This similarity is probably a case of parallel evolution, since all have somewhat restricted gill openings and hence the need of a solid opercular bone on which to insert strong pumping muscles. The posterior position of the suboperculum also shows some similarity to the Myctophoidei.

The posterior interoperculum is also unusual. Doubtless it was backwardly displaced during evolution of the enormous posterior extension of the jaws.

GIGANTURIDAE

Branchiostegals. Absent.
Operculars. Complete and entire, without spines. In *Gigantura* operculum small, shaped like a down-curved petal; suboperculum a large triangle; interoperculum a small triangle located immediately below, instead of anterior to, the suboperculum. Because of the oblique suspensorium the anterior two-thirds of the operculum is in front of the suboperculum. Gill opening restricted slightly in *Bathyleptus*, considerably in *Gigantura*.
Hyoid arch. Absent (except for hyomandibular).
References. Regan (1925), Walters (1961).
Material examined. None.

Order SACCOPHARYNGIFORMES (MONOGNATHIFORMES)

Branchiostegals, gulars, operculars, and hyoid arch (except hyomandibular) absent in the adult. But a cartilaginous operculum, an interhyal, and a ceratohyal cartilage present in larvae. Gill openings restricted, latero-ventral or ventral, and longitudinal instead of vertical. The gills are small and hoop-like, circling the small pharyngeal slits. Three families. Fossils unknown.

Because of the absence of the branchiostegal series and hyoid arch little may be said, from their point of view, of the ancestry of the Saccopharyngiformes. But the presence of an interhyal and operculum, newly discovered in the larvae (Orton, 1963), enables one, in agreement with Berg (1948), to discount Tchernavin's views (1947, 1947*a*) that this order does not belong in the teleostomes. Comparison of Orton's figures with de Beer's (1937) of *Anguilla* shows the opercular element to be similar, but to appear earlier, and the hyoid arch to be of different conformation, but to be delayed in the formation of a hypohyal. (*See* Note 4, Addenda.)

Various suggestions have been made as to the derivation of this order from the Anguilliformes, Synbranchiformes, Myctophiformes, Gadiformes, and Syngnathiformes. Harry (1952) has recently indicated possible relationship to the whalefishes some of which share a curious spongy luminous tissue around the first dorsal and anal fin rays and anus. There are also similarities to the Giganturiformes (*see* discussions under that order). The leptocephalous larvae of Saccopharyngiformes indicate possible relationship to the elopoids, albuloids, and anguilliforms. Orton (1963) believed that the latter "show significant developmental resemblances to the eels."

SACCOPHARYNGIDAE

Branchiostegals. Apparently absent.
Hyoid arch. Apparently absent in adults. Cartilaginous interhyal and ceratohyal in larvae ascribed to this family.
References. Bertin (1934), Orton (1963), Tchernavin (1947, 1947*a*).
Material examined. None.

EURYPHARYNGIDAE

Branchiostegals. Apparently absent.
Hyoid arch. Apparently absent in adults. A cartilaginous interhyal and epihyal in larvae ascribed to this family.
References. Bertin (1934), Orton (1963), Tchernavin (1947, 1947*a*).
Material examined. None.

MONOGNATHIDAE

Branchiostegals. Apparently absent.
Operculars. Apparently absent in adults.
Hyoid arch. Apparently absent in adults.
References. Bertin (1937), Bertin and Arambourg (1958).

Acanthopterygii

Branchiostegals 1–26, nearly always acinaciform. Gulars absent. Epihyal and ceratohyal often sutured. Not infrequently, spines on opercular bones. Almost always with 4 external branchiostegals and the rest ventral or internal. Twenty-six orders.

The Acanthopterygii (and hence the Malacopterygii) as generally understood have been considerably modified herein. The following comprise the primary characters of this group (*note* that characters may secondarily revert to the primitive state or to another state): branchiostegals acinaciform and in the 4 external +X[1] internal or ventral pattern; gape of upper jaw bordered principally by the premaxillaries; retractores arcuum branchialium muscle; pelvics subthoracic or thoracic; and possibly the fusion of the inner pelvic ray to a radial[2]; scales ctenoid; physoclistous; without mesopterygoid arch. Characters which apparently developed after the origin of the group and which help characterize higher acanthopterygians include the following: epihyal and ceratohyal sutured together; spines on operculars, preoperculum, and suborbitals; protrusile premaxillaries; true fin spines.

Some etymological purists may wish to change the name of the supraordinal category, Acanthopterygii, now that its bounds have been changed by inclusion of certain soft-rayed fishes. However, the Acanthopterygii already included taxa lacking spiny rays. To me it seems preferable to retain a well-used name.

Order MYCTOPHIFORMES

Pl. 12

Branchiostegals 6–26 with 2–14 epihyal, 3–10 ceratohyal, and 0–2 hypohyal, (0, 3) 4 (5, 14) external and (2, 3) 4 (5–17) internal (or ventral), all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present. Epihyal and ceratohyal not sutured. Opercular bones complete and entire. Gill membranes separate. Upper Cretaceous to present. Fifteen living and 3 fossil families making a total of 18, grouped in two suborders.

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[1] X = 0 to 17.

[2] Interestingly this condition is found in the Leptolepiformes (Rayner, 1937, fig. 13B).

The myctophiforms have been grouped amongst the malacopterygian fishes. The branchiostegal form and the 4 + X pattern, however, suggest placement in the acanthopterygians. Other recently discovered characters also firmly link the myctophiforms with the acanthopterygians: the possession of the retractores arcuum branchialium; an inner pelvic ray fused to a radial (not in all); the possession of an oval (" . . . like that found in various ganoid, macrourid and spiny-finned fishes.") and the euphysoclistous gas bladder (Marshall, 1960); the upper jaw bordered solely by the premaxillary; the usually thoracic or subthoracic position of the pelvics; the absence of a mesocoracoid arch; and the possession of ctenoid scales by members of many families (often ignored in the placement of this order, e.g., in Aulopidae, Chlorophthalmidae, Ipnopidae, Myctophidae).

The lack of spines, non-protrusible upper jaw (though premaxillary may have sizable ascending process), numerous caudal and pelvic rays, and presence of fulcral scales (*Aulopus*) indicate placement of the Myctophiformes near the root of the acanthopterygians.

The myctophiforms are therefore considered to be primitive acanthopterygians sharing a common ancestry with the ctenothrissiforms and beryciforms.

The possession of a high number of branchiostegals and caudal rays, the possession of fulcral scales (*Aulopus*), gular fold (*Bathypterois*), 3 epurals, 2 postterminal centra, and other characters in some members are evidence for derivation from an ancestor (at least) as primitive as the Elopoidei.

The division of the families into two suborders followed here is that of Marshall (1955).[1] There appear to be several basic types of branchiostegal arrangement: a) branchiostegals numerous, (9)11–26, with 6–9 on the epihyal and lacking the 4 external + X internal (ventral) pattern—Aulopidae, Synodontidae, Harpadontidae; b) branchiostegals fewer, 6–11, with 2–5 epihyal and 4 (3–5) external + X internal pattern which subdivides into two groups; c) 2 on the epihyal—Myctophidae and Neoscopelidae; d) 3–5 on the epihyal—Notosudidae, Chlorophthalmidae, Ipnopidae, Bathypteroidae, Paralepididae, Anotopteridae, Alepisauridae, Scopelarchidae, Evermannellidae, Scopelosauridae, and Omosudidae.

Group a) contains the most primitive myctophiforms. Possibly the Bathypteroidae also belong with them. The primitive characters of group a) and its lack of the 4 + X pattern may necessitate the exclusion of group a) from this order. Group c) is more primitive in that its members have a gas bladder. The members of group c) are united with one another and differentiated from the other groups by the possession of a gas bladder, of photophores, and of but two epihyal branchiostegals. According to Frost (1926) the myctophid sagitta differs from those of other myctophoids.

Suborder **Myctophoidei**

AULOPIDAE

Branchiostegals. Vary from (9)13–16 with 7–8 epihyal and 6–8 ceratohyal. *Aulopus japonicus* 13–15 long, slender, acinaciform branchiostegals which turn up around the posterior margin of the gill cover with 7 epihyal and 6–8 ceratohyal. *A. filamentosus* 15 with 8 epihyal and 7 ceratohyal. †*Sardinoides* about 9.

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[1] But Gosline, Marshall, and Mead (1966. Order Iniomi *in* Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res. (1) part 5: 1–18) no longer recognize subdivisions for the order. In accord with the views expressed here, these authors recognize the distinctiveness of the Myctophiformes from the Clupeiformes.

References. Bertelsen and Marshall (1956), Fowler (1936), Marshall (1955), Mead (1958).

Material examined. Aulopus japonicus, alcoholic specimen, USNM 51439, Japan; *Aulopus* sp., alcoholic specimen, USNM 135382, northwest Pacific.

†CHEIROTHRISSIDAE (CHIROTHRISSIDAE)

Branchiostegals. †*Cheirothrix* from at least 5 to 9, curved in semi-circle up behind gill cover.

Relationships. The shape and arrangement of the branchiostegals and the suboperculum would place this family in the Myctophoidei.

References. Davis (1887), Woodward (1901).

CHLOROPHTHALMIDAE

Pl. 12

Branchiostegals. Vary from 7–10 with 3–4 epihyal and 4–5 ceratohyal. *Chlorophthalmus nigripinnis, C. nigromarginatus, C. chalybeius, C. albatrossis, C. acutifrons*, and *C. oblongus* 8 with 3½–4 epihyal and 4–4½ ceratohyal. *C. nigripinnis* 8 with 4 external, 1 ventral, and 3 internal. All acinaciform in shape and curling up behind the suboperculum, some reaching the posterior notch in the suboperculum. A figure of 7 is also given for *C. nigripinnis* with 4 epihyal and 3 ceratohyal. *Chlorophthalmus agassizii* 8–10, *C. productus* 8, and *C. corniger* 8. *Bathysauropsis gracilis* 8–10 with 3 epihyal and 5 ceratohyal. Branchiostegal counts might suggest that *C. agassizii* belongs in *Bathysauropsis*, but Misra, Bertelsen and Marshall give the count of 8 for *agassizii*, and Günther gives 10.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in several species of *Chlorophthalmus*.

References. Bertelsen and Marshall (1956), Garman (1899), Günther (1887), Jordan and Evermann (1896), Misra (1953), Okada and Sano (1960), Weber and de Beaufort (1913).

Material examined. Chlorophthalmus nigripinnis, alizarin specimen, NMC62-245, New Zealand.

SCOPELOSAURIDAE

Branchiostegals. Vary from 9–10 with 3–4 epihyal and 5–6 ceratohyal in *Scopelosaurus*.

Relationships. See Marshall (1966, Family Scopelosauridae, p. 194–203, *in* the volume cited in the footnote, p. 90).

References. Bertelsen and Marshall (1956), Maul (1954), Weber and de Beaufort (1913).

Material examined. Scopelosaurus harryi, 2 alcoholic specimens, NMC65-300 and NMC66-22, off coast of British Columbia.

†DERCETIDAE

Branchiostegals. A few slender branchiostegals according to Woodward. *Benthesikyme* (*Leptotrachelus*) at least 7.
Relationships. Rhynchodercetis bears considerable resemblance to the nemichthyid-serrivomerid eels.
Reference. Woodward (1901).
Material examined. None.

BATHYPTEROIDAE

Branchiostegals. Vary from 11–14 with 4–5 epihyal and 7–8 ceratohyal. *Bathypterois* 11–14, *Benthosaurus* 11. *Bathypterois bigelowi, B. regis*, and *B. filiferus* 11, 4 on the epihyal and 7 on the ceratohyal. Branchiostegals curve up around behind gill cover. *Bathypterois guentheri* 12 with 4 epihyal and 8 ceratohyal. *B. atricolor* and *B. quadrifilis* 12 with 5 epihyal and 7 ceratohyal. *B. pectinatus* 12–13 with 4–5 epihyal and 8 ceratohyal.
Operculars. Complete. Gill membranes separate and covered by a transverse gular fold (*Bathypterois pectinatus*) or 'free from isthmus.'
References. Bertelsen and Marshall (1956), Fowler (1936), Garman (1899), Günther (1887), Jordan and Evermann (1896), Mead (1958*a*, 1959), Misra (1953).
Material examined. None.

IPNOPIDAE

Branchiostegals. Vary from 10–17 with 3–4 epihyal and 7 ceratohyal. *Ipnops* 10–12, *Bathymicrops* 11, *Bathytyphlops* 15–17. *Ipnops murrayi* 10 (other authors 12), 3 on the epihyal and 7 on the ceratohyal. *Bathymicrops regis* 11 with 4 epihyal and 7 ceratohyal. *Ipnops agassizi* 10. Branchiostegals swing up more than halfway behind gill cover.
References. Bertelsen and Marshall (1956), Garman (1899), Jordan and Evermann (1896), Mead (1958*a*), Weber and de Beaufort (1913).
Material examined. Ipnops murrayi, alcoholic specimen, USNM 101371, Gulf of Mexico at 24° N, 84° W.

HARPADONTIDAE

Branchiostegals. Vary from 11–26 with 14 epihyal and 9 ceratohyal. *Harpadon* 17–26, *Bathysaurus* 11–12. In *Harpadon*, at least, the branchiostegals curve up around behind the gill cover. *Harpadon nehereus* 23 with 14 epihyal and 9 ceratohyal, 14 external, 5 ventral, and 6 internal.
Hyoid arch. Interhyal, and a long epihyal, ceratohyal, and two hypohyals present.
Relationships. The marked difference in the number of branchiostegals might suggest that the placement of *Bathysaurus* be re-examined.
References. Alcock (1891), Bertelsen and Marshall (1956), Günther (1887), Jordan and Evermann (1896), Marshall (1955), Misra (1953), Weber and de Beaufort (1913).

Material examined. Harpadon nehereus, alcoholic specimen, NMC63-290, Singapore.

SYNODONTIDAE
Pl. 12

Branchiostegals. Vary from 12–18 with 6–8 epihyal and 9–10 ceratohyal, all ventral. *Synodus* 12–18, *Trachinocephalus* 16, *Saurida* 12–16. *Synodus foetens* 17 with 8 epihyal and 9 ceratohyal, all elongate acinaciform branchiostegals inserting along the ventral edge of the arch and curling up behind the gill cover. *Synodus scituliceps* 17 with 8 epihyal and 9 ceratohyal, all inserting on the ventral edge of the arch and curving up behind the gill cover. *Synodus lucioceps* 18 with 8 epihyal and 10 ceratohyal. *Saurida unosquamis* 16 with 6 epihyal and 10 ceratohyal.

Hyoid arch. Interhyal, epihyal, ceratohyal, and two hypohyals in *Synodus*.

References. Bertelsen and Marshall (1956), Day (1875), Fowler (1936), Garman (1899), Jordan and Evermann (1896), Marshall (1955, 1956). Matsubara and Iwai (1951), Meek and Hildebrand (1923), Misra (1953), Weber and de Beaufort (1913).

Material examined. Synodus scituliceps, alizarin specimen. Inst. Fish., University of British Columbia, Yavaros near Topolobampo, Mexico; *Synodus foetens*, alizarin specimen, NMC62-73, North Carolina.

MYCTOPHIDAE
Pl. 12

Branchiostegals. Vary from 8–10(12) with 2 epihyal, 5–6 ceratohyal, and 1–2 hypohyal, 4 external and 5 internal. *Myctophum* 8–12, *Tarletobeania* 8–10(11), *Scopelopsis* 10, *Lampadena* 9–10, *Lampanyctus* 9, *Electrona* 8, *Benthosema* 9, †*Dactylopogon* 12. *Tarletobeania crenularis* and *T. taylori* 9 with 2 epihyal, 5 ceratohyal, and 2 hypohyal, 4 external and 5 internal; *Diaphus theta* 9 with 2 epihyal, 6 ceratohyal, and 1 hypohyal, 4 external and 5 internal; *Electrona antarctica* and *E. carlsbergi* 8 with 2 epihyal and 6 ceratohyal; *Benthosema glaciale* 9 with 2 epihyal, 6 ceratohyal, and 1 hypohyal; *Myctophum humbolti* 8 with 2 epihyal, 5 ceratohyal, and 1 hypohyal; *Lampanyctus crocodilus* and *Lampadena braueri* 9 with 2 epihyal, 5 ceratohyal, and 2 hypohyal; *Lampadena nitida* and *Scopelopsis multipunctata* 10 with 2 epihyal, 6 ceratohyal, and 2 hypohyal. Branchiostegals acinaciform, do not curve up around the posterior border of the gill cover. In fifty *Tarletobeania crenularis* ten were found with 8 branchiostegals, thirty-four with 9, five with 10, and one with 11.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Tarletobeania* and *Diaphus.* Photophores are borne by the outer face of the hyoid arch, e.g., in *Myctophum evermanni* 3 with one on the lower epihyal, one on the middle of the ceratohyal, and one above the hypohyal.

Relationship. The high number of branchiostegals in †*Dactylopogon* exceeds that of most other myctophids.

References. Bertelsen and Marshall (1956), Fowler (1936), Fraser-Brunner

(1949), Garman (1899), Maul (1946), Smitt (1895), Weber and de Beaufort (1913), Woodward (1901).

Material examined. Tarletobeania taylori, alizarin specimen, NMC60-308-S, off British Columbia or Washington; alizarin specimen, BC58-324, off British Columbia or Alaska; *Tarletobeania crenularis*, 50 alcoholic specimens, BC60-170, off British Columbia; *Diaphus theta*, alizarin specimen, NMC60-308, off British Columbia.

NEOSCOPELIDAE

Branchiostegals. Vary from 8–10(11) with 2 epihyal, 6 ceratohyal, and 0 hypohyal. *Solivomer* 10(11), *Neoscopelus* 8–9, *Scopelengys* 8. *Solivomer arenidens* twenty-eight specimens with 10 and one with 11 branchiostegals. Bertelsen and Marshall report *Neoscopelus macrolepidotus* 9 with 4 epihyal and 5 ceratohyal and *Scopelengys tristis* 8 with 4 epihyal and 4 ceratohyal. But a specimen of the latter examined by the author had 2 epihyal branchiostegals and 6 ceratohyal, 4 external and 4 internal on both sides. Since 2 epihyal were found on both sides of the specimen and since only 2 were found in the closely related family Myctophidae, the counts of 4 on the epihyal should be verified.

Relationships. Some authors include the Neoscopelidae as a subfamily of the Myctophidae (Fraser-Brunner, Miller). Marshall (1955) is followed in recognizing it as distinct. The Myctophidae examined have branchiostegals on the hypohyal whereas the Neoscopelidae examined do not.

References. Fraser-Brunner (1949), Marshall (1955), Maul (1946), Miller (1947), Misra (1953), Weber and de Beaufort (1913).

Material examined. Scopelengys tristis, alcoholic specimen, BC62-150, Baja California, Mexico.

†ICHTHYOTRINGIDAE

Branchiostegals. In *Ichthyotringa* (as *Rhinellus*) Woodward reports 9, Davis 5, acinaciform.

Relationships. The generic name *Rhinellus* Agassiz 1840 proposed for this fish group is preoccupied by the amphibian genus *Rhinellus* Bonaparte 1831 (the latter proposed for *Rhinella* Fitzinger 1826). In 1878 Cope proposed a new name *Ichthyotringa* for a related fish fossil. Authors (e.g., Romer, 1955; White and Moy-Thomas. 1941) now consider *Ichthyotringa* Cope congeneric with *Rhinellus* Agassiz. The family name Rhinellidae used for this group must thus be replaced by Ichthyotringidae, which has as its type-genus *Ichthyotringa* Cope (article 39 of Int. Code Zool. Nomencl.).[1]

The elongate beak-like jaws of this group would appear to distinguish it from all other members of the suborder, indeed of the order. The apparent condition of the suboperculum, as noted above, would favour its inclusion in the Myctophoidei rather than in the Alepisauroidei.

References. Cope (1878), Davis (1887), Woodward (1901).

Material examined. None.

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[1] Obruchev (1964. Osnovi paleontologii. Bescheliostnie, ribi. Moscow, 522 p.) on p. 418 uses the name Ichthyotringidae, apparently for the first time.

Suborder Alepisauroidei

SCOPELARCHIDAE

Branchiostegals. Vary from 6–8, usually 8, with 4 external epihyal and 4 ventral ceratohyal. *Scopelarchus* 8, *Neoscopelarchoides* 8, *Promacheon* 6. *Scopelarchus anale* 8 with 4 external epihyal and 4 internal ceratohyal. The upper branchiostegal is somewhat apart from the others and slightly expanded. *Scopelarchus guentheri* 8 with 4 epihyal and 4 ceratohyal; *Neoscopelarchoides dubius* and *N. elongatus* 8 with 4 epihyal and 4 ceratohyal; *N. dentatus* with 4 external epihyal and 4 ventral ceratohyal.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals, all ends surfaced with cartilage.

References. Bertelsen and Marshall (1956), Parr (1929), Weber and de Beaufort (1913).

Material examined. Neoscopelarchoides dentatus, alcoholic specimen, NMC 65-301, off Queen Charlotte Islands, B. C.

EVERMANNELLIDAE

Branchiostegals. Evermannella with 8. *Evermannella indica* and *E. balbo* 8 with 4 on the epihyal and 4 on the ceratohyal.

Operculars. Complete and entire in *Evermannella*; interoperculum small.

Hyoid arch. Stated to be "normal."

References. Bertelsen and Marshall (1956), Günther (1887), Misra (1953), Parr (1929), Weber and de Beaufort (1913).

Material examined. None.

PARALEPIDIDAE (SUDIDAE)

Branchiostegals. Vary from 6–9 with 3–4 epihyal and 4–5 ceratohyal, (3) 4 external and 4 internal. *Sudis* 7–9, *Paralepis* 7–8, *Notolepis* 6–8, *Lestidium* 6–9, *Macroparalepis* 7–8, *Stemonosudis* 7. *Sudis hyalina* 7 with 3 epihyal and 4 ceratohyal. *Lestidium speciosum* 8 arranged in three separate groups: 2 very slender thread-like ones from the posterior corner of the outer epihyal, 2 from the outer surface of border between the epihyal and ceratohyal, and 4 from the inner surface of the ceratohyal. *Lestidium intermedium* 6, upper 2 missing. *Lestidium ringens* 8 with 4 external epihyal and 4 internal ceratohyal, with a gap between the second and third, the fourth and fifth, and the fifth and sixth; all acinaciform. *Paralepis coregonoides borealis* and *P. brevis* 7 with 3 epihyal and 4 ceratohyal, 3 external and 4 internal, all acinaciform. †*Holosteus* about 13.

Hyoid arch. Interhyal, epihyal, ceratohyal, and two hypohyals in *Lestidium ringens* and *Paralepis coregonoides borealis.*

Relationships. The gaps between certain of the branchiostegals appear to be characteristic of this family. †*Holosteus* has more branchiostegals than any other member known in the family and may not belong in it; it further differs in its edentulous upper jaw. There are certain similarities to the Beloniformes.

What is known of the branchiostegals does not disagree with this allocation.
References. Danilchenko (1960), Fowler (1936), Harry (1951, 1953), Jordan and Evermann (1896), Maul (1945, 1962), Misra (1953), Parr (1929).

Material examined. Lestidium sp., alcoholic specimen, BC55-36, Montega Bay, Jamaica; *Paralepis coregonoides borealis*, alcoholic specimen, NMC62-147, off Newfoundland; *Lestidium ringens*, alizarin specimen, NMC61-181, off Washington State.

ANOTOPTERIDAE

Branchiostegals. Vary from 7–9 in *Anotopterus*, with 4 epihyal and 3–5 ceratohyal. Hubbs, Mead and Wilimovsky report 7 rays in six specimens, Abe 8 rays, and Bertelsen and Marshall 9 rays. Hubbs *et al.* consider previous counts of 6 to have missed the small anterior ray; with this I concur. The five large upper rays are attached to the outer face of the arch, the lower ones to the internal; all are slender and acinaciform.

Hyoid arch. Interhyal, long epihyal, and ceratohyal present (hypohyals not examined).

References. Abe (1952), Bertelsen and Marshall (1956), Hubbs, Mead and Wilimovsky (1953), Kobayashi and Ueno (1956), Maul (1946).

Material examined. Anotopterus pharao, alcoholic specimen, BC58-403, weathership Stonetown, North Pacific.

ALEPISAURIDAE

Branchiostegals. Vary from 7–8 with 4 epihyal and 3–4 ceratohyal. *Alepisaurus* 7–8. *Alepisaurus aesculapius* 7 with 4 external epihyal and 3 internal ceratohyal. A gap exists between the ones on the epihyal and those on the ceratohyal. All acinaciform. *Alepisaurus ferox* 8 with 4 epihyal and 4 ceratohyal. Counts of 5 branchiostegals are regarded with doubt.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal about equal in length to ceratohyal.

References. Bertelsen and Marshall (1956), Fowler (1936), Jensen (1948), Jordan and Evermann (1896).

Material examined. Alepisaurus aesculapius, skull at Inst. Fish., University of British Columbia.

OMOSUDIDAE

Branchiostegals. Omosudis with 8. *Omosudis lowei* 8 with 4 on the outer surface of the epihyal and 4 on the inner surface of the ceratohyal.

Hyoid arch. At least epihyal and ceratohyal present.

References. Bertelsen and Marshall (1956), Fowler (1936), Günther (1887), Jordan and Evermann (1896), Parr (1929).

Material examined. None.

Order CETOMIMIFORMES[1]

Pl. 12

Branchiostegals 7–10 with 3–4 epihyal and 4–5 ceratohyal, 4 external and 4 ventro-internal, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present. Epihyal and ceratohyal not sutured. Ceratohyal with developed or reduced beryciform foramen. Operculars complete and entire. Gill membranes separate or united and free. Fossils unknown. Three families.

The whalefishes, comprising the three families (or subfamilies), have been accorded different ordinal placement. Goode and Bean (1896) placed them in the Iniomi (= Myctophiformes); Jordan (1923) placed them in their own order Cetunculi; Parr (1929, 1945) placed the Rondeletiidae in the Xenoberyces and the Cetomimidae and Barbourisiidae in the Iniomi; Matsubara (1955) placed them in a distinct order Cetomimida; Bertin and Arambourg (1958) placed them in the Stephanoberyciformes; Berg (1947) placed the Rondeletiidae in the Stephanoberyciformes and the Cetomimidae in the Myctophiformes. Harry (1952) suggested relationship between the whalefishes and the Saccopharyngiformes. He also believed that the whalefishes deserved at least subordinal status. Parr (1929, 1945) and Harry (1952) have granted each of the three groups familial status, whereas Myers (1946) considered the Barbourisiidae only a subfamily of Cetomimidae. The latest author, Harry, is here followed in according each of the three groups familial status. The differences in vertebral number are suggestive of familial differentiation: Cetomimidae 51–52, Barbourisiidae 42, Rondeletiidae 27.

The degenerate condition of these fishes and lack of knowledge on certain features made placement difficult.[2] The branchiostegal form and pattern, the presence of a supposedly beryciform foramen in the ceratohyal, and the bordering of the upper jaw solely by the premaxillary are characters suggesting placement in the Acanthopterygii. The thumb-tack scales, each bearing a central spine, in *Barbourisia* may represent modified ctenoid scales. Although they do differ from them, affinities are shown with certain of the alepsauroid Myctophiformes and the Mirapinniformes; the supposedly beryciform foramen suggests relation to or derivation from the Beryciformes. The number of branchiostegals on the epihyal, 3 to 4, is higher than in most acanthopterygians. The total number is characteristic of primitive acanthopterygians as are the projections on the bases of the upper three branchiostegals in *Rondeletia*. The possession of up to 17 branched caudal rays and the presence of intermuscular bones are also primitive features in the Acanthopterygii. A number of more specialized features are apparently related to life in the deep sea: coloration; bones not completely ossified; highly developed lateral line systems; luminous tissue; and so on.

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[1] G.S. Myers and W.C. Freihofer (1966. Megalomycteridae, a previously unrecognized family of deep-sea cetomimiform fishes based on two new genera from the North Atlantic. Stan. Ichthyol. Bull. 8: 193–207, 5 fig.) erect a new family and a new suborder (Megalomycteroidei). This family has 8–9 acinaciform branchiostegals with 4–5 epihyal and 4 ceratohyal, 3–4 external (in the figure); the gill membranes are separate or united and free. An interhyal, operculum, and interoperculum are also figured, but no suboperculum. The branchiostegal data are commensurate with placement in the Cetomimiformes.

[2] But Dr. Y. Tominaga, University of Tokyo, is undertaking an osteological study of *Rondeletia*.

BARBOURISIIDAE[1]

Pl. 12

Branchiostegals. 8 in *Barbourisia rufa* (7 reported by Parr, 1945) with 3 epihyal and 5 ceratohyal, 4 external and 4 ventro-internal, all acinaciform, none with anterior basal projections. The body, including the branchiostegal membranes, is covered by extremely close-set, thumbtack-like scales.

Hyoid arch. Consists of interhyal, epihyal, rather slender ceratohyal, and two hypohyals. Cartilage separates the hypohyals from the ceratohyal and the ceratohyal from the epihyal. But a slender thread of bone may unite the last two. Above the longitudinal ridge on the ceratohyal are two small perforations which probably represent an obsolescent beryciform foramen.

References. Abe and Maruyama (1963), Parr (1945).

Material examined. Barbourisia rufa, alizarin-stained hyoid arch with branchiostegal rays, from Japan, kindly lent by Dr. T. Abe.

RONDELETIIDAE

Branchiostegals. Rondeletia bicolor 7–8 with 4 on the outer epihyal and 4 on the inner surface of the ceratohyal; *R. loricata* 8 with 3 epihyal and 5 ceratohyal, 4 external and 4 ventro-internal, all acinaciform with slight projections on the anterior bases of the upper three.

Hyoid arch. Consists of interhyal, epihyal, fairly deep ceratohyal, and two hypohyals. The epihyal and ceratohyal appear to be joined by a slender strand of bone, but no other sign of suturing exists. A small beryciform foramen is present above the strong longitudinal ridge on the ceratohyal.

References. Abe and Hotta (1963), Goode and Bean (1896), Parr (1929).

Material examined. Rondeletia loricata, alizarin-stained hyoid arch with branchiostegal rays, from Japan, kindly lent by Drs. T. Abe and Y. Tominaga.

CETOMIMIDAE

Branchiostegals. Vary from 8–10. *Ditropichthys storeri* 8 with 4 epihyal and 4 ceratohyal. *Cetostoma regani* 8, *Cetomimus gilli* 9, and *C. compunctus* 10[2] (on both sides).

Hyoid arch. Said to be strongly developed in *Cetostoma*.

References. Bertelsen and Marshall (1956), Goode and Bean (1896), Parr (1929).

Order MIRAPINNIFORMES

Pl. 13

Branchiostegals 7–9 with 3–5 epihyal and 4 ceratohyal, 4–5 external and 4 ventral (or free), all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present. Ceratohyal without foramen. Operculars complete and entire. Gill membranes separate. Three families. Fossils unknown.

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[1] P. Struhsaker also reports 8 branchiostegals (1965. The whale fish *Barbourisia rufa* (Cetunculi) from waters off southeastern United States. Copeia (3): 376–377, 1 fig.).

[2] *See* Abe, T. R. Maruno, and K. Kawaguchi, 1965. Description of a new cetomimid fish from Suruga Bay. Japanese J. Ichthyol. 12 (3/6): 57–63, 2 figs.

Bertelsen and Marshall (1958) created the order Miripinnati for the two families below. They concluded that there were evident affinities with the Cetunculi and Chondrobrachii. Bertin and Arambourg (1958) reduced it to a suborder, Miripinnatoidei, between the myctophoids and ateleopoids.

Because of their degenerate condition and the lack of specimens for detailed study, evidence for placement is inadequate. However, the premaxillary bordered jaws, slightly protrusible premaxillaries, jugular pelvics, and 4 + X branchiostegal pattern are characters suggesting acanthopterygian placement, and the physoclistous larval gas bladder agrees with this. The absence of fin spines, if primary, would suggest placement among the lower acanthopterygians. Mirapinniformes are placed here close to the Cetomimiformes, as suggested by Bertelsen and Marshall, although they might be related to the Ateleopiformes or Ophidiiformes. Inclusion of this order in Berg's classification required the coining of a replacement name for Miripinnati, Mirapinnatiformes, which was done by Robins and de Sylva (1965).

MIRAPINNIDAE

Branchiostegals. Marapinna esau 8 with 4 on the outer surface of the epihyal and 4 on the ceratohyal, all acinaciform. The upper branchiostegals curve parallel with the suboperculum up behind the operculum.
Hyoid arch. At least interhyal, epihyal, and ceratohyal present.
Reference. Bertelsen and Marshall (1956).
Material examined. None.

EUTAENIOPHORIDAE (TAENIOPHORIDAE)

Pl. 13

Branchiostegals. Vary from 7–9 with 3–5 epihyal and 4 ceratohyal.
Eutaeniophorus festivus 8–9 with 4 epihyal and 4 ceratohyal in sixteen specimens and 5 epihyal and 4 ceratohyal in five specimens. *Parataeniophorus gulosus* 7–9 with 4 epihyal and 4 ceratohyal in eleven specimens, 5 epihyal and 4 ceratohyal in one specimen, and 3 epihyal and 4 ceratohyal in one specimen; those on the epihyal being on its external face; *P. brevis* 8 with 4 epihyal and 4 ceratohyal. Branchiostegals in all species acinaciform and curving up behind operculum.
Hyoid arch. In *Eutaeniophorus* consists of interhyal, epihyal, ceratohyal, and two hypohyals.
Reference. Bertelsen and Marshall (1956, 1958).

KASIDORIDAE[1] (KASIDOROIDAE)

Branchiostegals. Kasidoron edom 9, apparently 4 epihyal and definitely 5 ceratohyal, acinaciform.
Hyoid arch. At least epihyal and ceratohyal present.

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[1] Dr. C. Richard Robins kindly permits me to add the following points from his MS. on the structure and relationship of the family.—There are definitely 4 external epihyal and 5 ventral ceratohyal branchiostegals. There is a small (presumably beryciform) foramen in the ceratohyal. This and the branchiostegal arrangement further favour placement of this family and order in the Actinopterygii. The epihyal, ceratohyal, and hypohyals are separated by cartilage, there being no sutures.

References. Added just before manuscript was given to editor. Robins, Richard C., and Donald P. de Sylva (1965). The Kasidoroidae, a new family of mirapinniform fishes from the Western Atlantic Ocean. Bull. Marine Sci., U. Miami 15(1): 189–201, 2 figs.

†Order CTENOTHRISSIFORMES

Pl. 13

Branchiostegals 9 with 2–3½ epihyal and 5½–7 ceratohyal, 4 external and 5 internal or ventral, all acinaciform. Two hypohyals, a short deep ceratohyal with beryciform foramen, epihyal, and interhyal. Epihyal and ceratohyal sutured together or not. Opercular bones complete and entire. Upper Cretaceous. Two families, both known only from fossils.

This group was first placed with the berycoids. Regan and Berg placed it close to the clupeoids. Bertin and Arambourg (1958) placed the Ctenothrissidae in the Bathyclupeiformes. Although the Ctenothrissidae agree superficially in body form with the Bathyclupeiformes, they differ strongly by their lack of fin spines and ventrals with 15 rays and by their possession of two supramaxillaries, 17 branched caudal rays, and 9 branchiostegals. The possession of a rostral indicates placement in or below the Clupeiformes, according to Gardiner (1963).

The attainment of a number of spiny-rayed fish characters indicates placement in the acanthopterygians: the form and arrangement of the branchiostegals, the beryciform foramen in the ceratohyal, the ctenoid scales (Ctenothrissidae), the sutured epihyal and ceratohyal (Ctenothrissidae), the suborbital shelf, the thoracic ventral fins. The retention of several primitive characters (e.g., retention of rostral and orbitosphenoid) and the primitive absence of some of the characters not found in higher spiny-rayed fishes indicates that it should be placed at the base of the acanthopterygians. The retention of primitive characters does not prevent inclusion of families into orders otherwise lacking them, so long as the family also possesses the diagnostic features of that order, e.g., a gular plate does not preclude the Elopoidei from the Clupeiformes.

Patterson (1964) indicates that the ctenothrissids are excluded from the direct ancestry of other acanthopterygians by their reduced dentition.

†AULOLEPIDAE

Branchiostegals. At least 8 in *Pateroperca. Aulolepis* 9 with 3½ epihyal and 5½ ceratohyal, apparently 4 (at least 3) external and 5 ventral. The upper 4 'blade-shaped,' the lower 5 slender, curved, and rod-like.

Hyoid arch. Consists of interhyal; epihyal; perforate, deep ceratohyal; two hypohyals. Epihyal and ceratohyal separate.

Reference. Patterson (1964).

†CTENOTHRISSIDAE

Pl. 13

Branchiostegals. Ctenothrissa 9 broadly acinaciform with 2 epihyal and 7 ceratohyal, lower 5 internal and upper 4 apparently external.

Hyoid arch. Consists of interhyal; epihyal; short, deep, and perforate ceratohyal; two hypohyals. The epihyal and ceratohyal are weakly but definitely sutured together.

References. Patterson (1964), Woodward (1901, 1902–1912).

Order BERYCIFORMES (STEPHANOBERYCIFORMES)

Pl. 12

Branchiostegals (5?) 7–9 (10) (12?) with 2 (3) epihyal (but Bertelsen and Marshall report 1–3) and 2–7 ceratohyal (and 3 or 4 hypohyal in Polymixiidae), 4 external and 4 ventral, all acinaciform, relatively broad, sometimes with an anterior oval prolongation of the base of some of the upper branchiostegals. Two hypohyals, a short ceratohyal usually with a beryciform foramen, a short epihyal, and an interhyal. Epihyal and ceratohyal separate, not sutured together. Opercular bones complete, with or without spines. Suboperculum and interoperculum may have series of small spines. Gill membranes separate. Upper Cretaceous to present. Nineteen families included, five of which are known only from fossils.

According to Katayama (1960), *Ostracoberyx*, which Berg (1947) includes as the Ostracoberycidae in the Beryciformes, belongs in the Serranidae; Katayama is followed. The Trachyberycidae, previously considered beryciforms, are probably bramids (Mead and Maul, 1958). Regan (1911) revised the order.

According to Regan (1929) this order is directly intermediate between the clupeoids and the Perciformes. Frost (1927) found the sagitta of Holocentridae to be similar in general form to that of *Elops* but the sulcus to be distinctly percoid. According to Gosline (1961) the caudal skeletons of the basal berycoids are nearer the basal clupeiform type (*Albula*) than are those of *Clupea*. Gosline (1963*a*) derives the beryciforms from the myctophiforms. The berycoids have the iniomous expansion of the inner pelvic radial.

The author agrees with Regan that these fishes are intermediate in some characters between the malacopterygians and most acanthopterygian fishes, although they definitely belong in the acanthopterygian group. The following characters of the beryciforms are primitive: 1–2 supramaxillaries; orbitosphenoid usually present; 16–17 branched caudal rays; numerous pelvic rays; a postterminal centrum in primitive families; fairly numerous branchiostegal rays (7–9). On the other hand, most acanthopterygian characters are present: the form and arrangement of the branchiostegals; the upper jaw bordered by the premaxillary alone; the ctenoid scales and true fin spines; the physoclistic gas bladder; the subocular shelf; the protrusible premaxillaries; and the presence of opercular spines. These characters indicate definite acanthopterygian placement.

Regan (1911) created a new order for the families Melamphaidae and Stephanoberycidae which he thought were derived from the berycoids but which differed from them by the toothless palate, by the absence of a subocular shelf, by the triangular shape of the single supramaxillary, and by the absence of an orbitosphenoid. (Possibly the Gibberichthyidae might also now be considered related to this group.) However, later (1929) he withdrew this order and provisionally included the Melamphaidae and the Stephanoberycidae amongst the Berycomorphi. The latter action has not been followed by Berg nor by Bertin and Arambourg (1958). Patterson (1964) did not include them in his review of the Beryciformes. The branchiostegal number and pattern would indicate that these families are related to the Beryciformes. The possession of a perforate ceratohyal by the Melamphaidae would also indicate that they belong with other Beryciformes. Since the characters by which this group of families differ are chiefly ones of degeneration, perhaps related to a bathypelagic existence, and since there is good evidence of beryciform affinity, it might seem preferable to include them within the Beryciformes, possibly as a suborder. (However, data are lacking on the Gibberichthyidae.)

In the Beryciformes examined a suture is lacking between the epihyal and the ceratohyal. However, the suture is known in the Zeiformes and the Perciformes, both of which are descended from the Beryciformes or their close ancestors, as well as in the related Ctenothrissiformes. It therefore might be supposed that the immediate ancestors of the Beryciformes, from which these three orders descended, possessed an epi-ceratohyal suture. The suture would then have been secondarily lost in the Beryciformes (as they have become lost in some representatives of other acanthopterygian orders).

Patterson's (1964) subordinal arrangement of the Beryciformes is followed here, except that the Stephanoberycoidei is included.

Suborder **Polymixioidei**

†SPHENOCEPHALIDAE

Branchiostegals. At least 7, probably 8, in †*Sphenocephalus*.
Hyoid arch. Includes a ceratohyal perforated by a large oval beryciform foramen.
Reference. Patterson (1964).
Material examined. None.

POLYMIXIIDAE (BERYCOPSIDAE)

Branchiostegals. Polymixia with either 7 or 8 (counting barbel splints), the posterior 4 being regular acinaciform branchiostegals with 1½ on the epihyal and 2½ on the ceratohyal, these 4 being on the external face of the hyoid arch and having slightly enlarged bases. An attenuate barbel arises from the posterior corner of the lower hypohyal. Around the base of this barbel are three small, curved splints which support it. These splints, according to Starks (1904*a*), are homologous with branchiostegals. This theory explains why *Polymixia* apparently has only 4 branchiostegals although all other beryciforms have 7 or 8. There is a further possibility that the barbel itself represents a modified branchiostegal, although its form does not suggest this. †*Homonotichthys* 4 (anterior one reduced and modified as a barbel), †*Pycnosterinx* about 5, †*Berycopsis* 8. †*Omosoma* has been described as having a dozen branchiostegals (Arambourg, 1954), but Patterson (1964) later credits it with only 8 acinaciform branchiostegals.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Polymixia*; epihyal and ceratohyal separate. Ceratohyal imperforate in *Polymixia*, †*Pycnosterinx*, and †*Homonotichthys*.

Relationships. Because the Mullidae also have hyoid barbels and a branchiostegal count of four, authors have suggested that the two families are related. However, Starks (1904*a*) has pointed out that the barbel structure is basically different. Since other structures do not support the nearness of the families, the Mullidae should not be placed in the Beryciformes. Patterson (1964) includes the Berycopsidae in the Polymixiidae.
References. Davis (1887), Fowler (1936), Jordan and Evermann (1896), Lachner (1955), Patterson (1964), Starks (1904*a*), Woodward (1901, 1902–1912).
Material examined. None.

†Suborder **Dinopterygoidei**

†DINOPTERYGIDAE

Branchiostegals. 8 in *Dinopteryx.*
Reference. Patterson (1964).
Material examined. None.

†PYCNOSTEROIDIDAE

Branchiostegals. 8 in *Pycnosteroides.*
Hyoid arch. Ceratohyal with oval beryciform foramen.
Reference. Patterson (1964).
Material examined. None.

†AIPICHTHYIDAE

Branchiostegals. 8–10 in *Aipichthys* with 4 lateral and 4 internal.
References. Patterson (1964), Woodward (1901, 1902–1912).
Material examined. None.

†PHARMACICHTHYIDAE

Branchiostegals. At least 6 in *Pharmacichthys.*
Reference. Patterson (1964).
Material examined. None.

Suborder **Berycoidei**

BERYCIDAE

Branchiostegals. 8, sometimes 7 or 9, in *Beryx. Beryx splendens* 7 with 2 on the epihyal and 5 on the ceratohyal. Branchiostegals curved, fairly broad, acinaciform.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in *Beryx*; the ceratohyal is perforated by an oval beryciform foramen.
References. Abe (1959), Günther (1887), Jordan and Evermann (1896), Maul (1954), Smitt (1892), Starks (1904*a*), Woodward (1901, 1902–1912).
Material examined. None.

HOLOCENTRIDAE (MYRIPRISTIDAE)

Pl. 12

Branchiostegals. Usually 8, rarely 7. *Holocentrus* 8; †*Caproberyx* 8; *Myripristis* 8, exceptionally 7; †*Trachichthyoides* with at least 6. *Holocentrus suborbitalis* and *H. diadema* 8 with 2 epihyal and 6 ceratohyal, 4 external and 4 on the ventral face of the hyoid arch, all acinaciform, upper 4 with slightly enlarged bases. *Holocentrus ascensionis* 8 with 2 epihyal and 6 ceratohyal. †*Caproberyx superbus* 8 with 4 large external and 4 small ventro-internal.

Hyoid arch. In *Holocentrus* consists of an interhyal, a broad epihyal and ceratohyal, and two hypohyals. Epihyal and ceratohyal separate. Groove on outer face of epihyal and ceratohyal. Ceratohyal imperforate. In †*Caproberyx* interhyal not yet seen; epihyal, perforate ceratohyal, and two hypohyals present.

References. Day (1875), Fowler (1936), Hubbs (1920), Meek and Hildebrand (1923), Patterson (1964), Starks (1904*a*), Weber and de Beaufort (1929).

Material examined. Holocentrus suborbitalis, alizarin specimen, BC60-17, Acapulco, Mexico; *Holocentrus diadema*, alizarin specimen, NMC63-120, Hawaii.

TRACHICHTHYIDAE (KORSOGASTERIDAE)

Branchiostegals. Constantly 8. †*Hoplopteryx* 8, †*Acrogaster* 8, *Hoplostethus* (incl. *Leiogaster*) 8, *Gephyroberyx* 8, *Korsogaster* 8, *Trachichthys* 8. *Hoplostethus intermedius* 8 with 2 epihyal and 6 ceratohyal, 4 external and 4 ventral, all acinaciform, the uppermost with an oval elongate base, the next three with slightly enlarged bases. *Hoplostethus japonicus* 8 with 2 epihyal and 6 ceratohyal. †*Hoplopteryx lewesiensis* 8, 4 broad external and 4 slender internal; same in *H. simus* except anterior edges of 4 anterior ones are serrated.

Hyoid arch. Consists in *Hoplostethus* and †*Hoplopteryx* of interhyal, broad epihyal and ceratohyal, and two hypohyals; ceratohyal with central oval beryciform foramen.

References. Fowler (1936), Garman (1899), Jordan and Evermann (1896), Maul (1954), Parr (1933*a*), Patterson (1964), Starks (1904*a*), Weber and de Beaufort (1929), Woodward (1902–1912).

Material examined. Hoplostethus intermedius, alizarin specimen, NMC62-245, New Zealand.

ANOPLOGASTERIDAE (CAULOLEPIDAE)

Branchiostegals. Anoplogaster (=*Caulolepis*) 8. *A. cornutus* 8 with 3 epihyal and 5 ceratohyal, 4 external and 4 ventral, all acinaciform.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals.

References. Fowler (1936), Günther (1887), Maul (1954).

Material examined. Anoplogaster cornutus, alcoholic specimen, BC62-164, south of Guadalupe Island, Mexico.

DIRETMIDAE

Branchiostegals. Diretmus argenteus 7–9.
References. Abe (1953*a*), Fowler (1936), Johnson (1863), Koefoed (1953), Maul (1949).
Material examined. None.

SOROSICHTHYIDAE

Branchiostegals. 7 in *Sorosichthys.*
Taxonomy. Family erected by Whitley. Patterson includes it in the Berycoidei and considers it related to the Trachichthyidae.
References. Patterson (1964), Whitley (1945).

PARADIRETMIDAE

Branchiostegals. Not described for *Paradiretmus.*
Taxonomy. Family erected by Whitley (1951); considered doubtfully placeable in the Beryciformes by Patterson (1964). Provisionally left there.
Reference. Whitley (1948).

CARISTIIDAE (ELEPHANORIDAE)

Branchiostegals. Platyberyx (5?) 7, *Caristius* 7. Maul gives a count of 7 for *Platyberyx opalescens,* a number which would appear normal for the family; but Koefoed and Fowler give a count of 5. Whether the latter authors have missed two rays in their counts (which seems most likely) or whether some specimens actually have 5 rays is not certain.
References. Fowler (1936), Koefoed (1953), Maul (1949).
Material examined. None.

ANOMALOPIDAE

Branchiostegals. 8 in *Anomalops* and *Photoblepharon.*
References. Bertin and Arambourg (1958), Weber and de Beaufort (1929).
Material examined. None.

MONOCENTRIDAE

Branchiostegals. Monocentris japonicus 8 with 2 epihyal and 6 ceratohyal, 4 external and 4 ventral, all acinaciform, the lower 3 but one spinulose with 3–7 spinules on centre of ventral side; the fourth with a percopsid projection.
Hyoid arch. Consists of large interhyal, ceratohyal, epihyal, and two hypohyals; the ceratohyal with an oval beryciform foramen.
Reference. Starks (1904*a*).
Material examined. Monocentris japonicus, alizarin specimen, NMC62-142 & S. South Africa.

Suborder **Stephanoberycoidei**

MELAMPHAIDAE

Branchiostegals. 8 in the genera *Melamphaës, Scopelogadus, Scopeloberyx,* and *Poromitra*; 7 in genus *Sio. Melamphaës lugubris* 8 with 2 epihyal and 6 ceratohyal, 4 external and 4 ventral, upper 2 crescentic, the rest acinaciform.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal separate. Ceratohyal with an oval beryciform foramen.

References. Garman (1899), Günther (1887), Moss (1962), Weber and de Beaufort (1929).

Material examined. Melamphaës lugubris, alizarin specimen, NMC61-187, Pacific Ocean at 47½° N, 146½° W.

STEPHANOBERYCIDAE

Branchiostegals. Stephanoberyx 7, *Malacosarcus* 8. According to Hubbs *Stephanoberyx* has the standard acanthopterygian pattern.

References. Goode and Bean (1896), Günther (1887), Hubbs (1920), Jordan and Evermann (1896).

Material examined. None.

GIBBERICHTHYIDAE

Branchiostegals. No data available.

Reference. Parr (1933*a*).

Material examined. None.

Order **LAMPRIDIFORMES**

Branchiostegals 5–7 with 0–3 epihyal and 3–5 ceratohyal, 4–6 external and 0–2 ventral. Opercular bones complete, entire, and without spines; gill openings separate or narrowly joined to isthmus. Interhyal, epihyal, ceratohyal, and one or two hypohyals present; the upper hypohyal, if present, above the anterior end of the ceratohyal; epihyal and ceratohyal not united by suture (although their borders may be serrate). Oligocene to present. Six families.

Boulenger (1904) considered the Lamprididae to be close to the Gasterosteidae. Regan (1907*a*) considered the Allotriognathi derivable from the Beryciformes. In *Velifer* (Frost, 1927) the principal otolith is fairly generalized and resembles that of the berycoid *Polymixia.* Gosline (1961) stated that the caudal skeleton of *Velifer* sets it to one side of the lineage leading to percoids. Gosline (1963*a*) questionably derives the lampridiforms from a myctophiform lineage. Patterson (1964) considers it likely that the Lampridiformes arose from dinopterygoid beryciforms. The absence of opercular spines, the presence of up to 17 branched caudal rays, the numerous soft pelvic rays, and the presence of an orbitosphenoid all indicate this order to be more primitive than other post-beryciform orders. The insertion of all the branchiostegals on the external face of the hyoid arch in the Regalecidae and

Stylephoridae is probably a secondary condition. The beryciform foramen in Stylephoridae is evidence for the placement of the order among primitive acanthopterygians.

Suborder **Veliferoidei**

VELIFERIDAE

Branchiostegals. 6 placed very close together in *Velifer* and *Metavelijer.* Counts of 4 are probably erroneous, as indicated by Walters.
References. Gregory (1933), Regan (1907, 1907*a*), Walters (1960).
Material examined. None.

Suborder **Lampridoidei**

LAMPRIDIDAE (LAMPRIDAE)

Branchiostegals. 6–7 acinaciform in *Lampris.*
References. Gregory (1933), Jordan and Evermann (1896), Regan (1907*a*), Smitt (1892).
Material examined. None.

Suborder **Trachipteroidei (Trachypteroidei)**

LOPHOTIDAE

Branchiostegals. 6 in *Eumecichthys.*
Reference. Abe (1954).
Material examined. None.

TRACHIPTERIDAE (TRACHYPTERIDAE, RADIICEPHALIDAE)

Branchiostegals. Trachipterus 6, perhaps rarely 7, with 3 epihyal and 3 ceratohyal, 4 on the external and 2 on the ventral face of the arch, all slender acinaciform, hidden by elongate interoperculum.
Hyoid arch. Interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal separate. Dorsal hypohyal lies above the anterior end of the ceratohyal. Cartilage lies between the lower hypohyal, ceratohyal, and epihyal. Arch short and wide.
References. Fitch (1964), Hubbs (1920), Jordan and Evermann (1896), Smitt (1892), Weber and de Beaufort (1929).
Material examined. Trachipterus altivelis, alizarin specimen, SU36830, Monterey, California.

REGALECIDAE

Branchiostegals. 6 with 1 epihyal and 5 ceratohyal. In *Regalecus argenteus* all, unusually for an acanthopterygian, on the external face of the hyoid arch, and slender acinaciform.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal with opposing edges serrate (remnant of a suture?) and separated by cartilage. Upper hypohyal extends over the dorsal edge of

the anterior end of the ceratohyal. Lower hypohyal separated from its neighbours by cartilage.
References. Benham and Dunbar (1906), Day (1875), Hubbs (1920), Parker (1890), Smitt (1892).
Material examined. None.

Suborder Stylephoroidei

STYLEPHORIDAE

Branchiostegals. Stylephorus 5, all on the external face of the ceratohyal, with the bases on the dorsal edge of the ceratohyal and their tips pointing upwards. This position, on the *upper* edge of the ceratohyal, is unique.
Hyoid arch. Consists of an anterior subrectangular epihyal, a rectangular ceratohyal with a ventral beryciform foramen, and a single posterior triangular hypohyal.

The unique placement of the branchiostegals deserves some discussion.[1] Starks (1908) considered the hyoid elements to be in their normal position with the anteriormost element being the hypohyal and the posteriormost the epihyal. If this interpretation is true then the branchiostegals must have migrated across the anterior face, from the lower to the upper edge, and turned through 180 degrees. Also, the first branchiostegal must have become smaller than the last (contrary to the usual condition).

However, another interpretation of the hyoid elements is possible. The hyoid arch is normally close to vertical in this order. If the lower end of the arch moved posteriorly the normally dorso-anterior edge of the arch would have become ventral and the branchiostegals would lie on the upper side. An impetus for such a movement of the arch is conceivable. The lower jaw in this suborder is enormously elongate. It is possible that during evolution of this elongate jaw the prolongation carried the lower end of the arch posteriorly and inverted it. Support for this theory lies in the shape of the ceratohyal in this suborder, concave above and convex below, and in the ventral position of the ceratohyal foramen. These conditions are the inverse of the normal. This theory also explains the odd dorsal position and size sequence of the branchiostegals. Evidence therefore favours interpretation of the arch as rotated forward. Thus Starks's "epihyal" is the hypohyal, and his "hypohyal" is the epihyal. A similar inverted position of the arch is found in stomiatoids when the lower jaw is thrown forward.
References. Fowler (1936), Hubbs (1920), Starks (1908).
Material examined. None.

Order ZEIFORMES

Pl. 13

Branchiostegals (5) 6–8 with 0–1 (4) epihyal and 2–8 ceratohyal, 4 external and 3–4 ventral, all acinaciform. Two hypohyals, a ceratohyal, an epihyal, and an interhyal present. Suture between the epihyal and ceratohyal. Ceratohyal with a beryciform foramen (foramen may lack upper border and open dorsally). Opercular bones complete and without spines; interoperculum sometimes spinulose. Gill membranes separate. Palaeocene to present. Seven families, one known only from fossils.

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[1] Meinel (1962, Naturwissenschaften 19: 453) discusses the interesting jaw suspension of this genus, which he calls tritohyostyly, but he does not discuss the lower hyoid elements.

Zeoids have been considered closely related to the chaetodonts (Starks, 1898, 1902). However, several characters show the zeoids to be more primitive than and not closely related to the chaetodonts: the high number of branchiostegals; the high number of vertebrae; the high number of pelvic rays. Further, the zeoids, unlike the chaetodonts, lack a subocular shelf, and so could not have given rise to them. The number and pattern of the branchiostegal rays and the perforated ceratohyal agree, on the other hand, with the Beryciformes. There is also agreement in the number of vertebrae, otoliths (Frost, 1927), pelvic rays, and other characters. Since the number of supramaxillaries, the caudal rays, the range of pelvic rays, and the range of branchiostegals is lower than in the Beryciformes and since the subocular shelf is present in the Beryciformes, the Zeiformes must be derived from the Beryciformes (or their close relatives), rather than vice versa. Gosline (1961, Fig. 4; 1963*a*) suggests that the Zeiformes arose from the Beryciformes; Regan (1910) had already evinced this opinion. Patterson (1964) considers that the Polymixioidei are possibly ancestral to the Zeiformes. The perforated ceratohyal is an important character in relating these groups.

The branchiostegal arrangement in the Caproidae is said to be 4 epihyal and 2 ceratohyal (Starks, 1902), and this differs considerably from that in other Zeiformes where it is 0–1 epihyal and 6–8 ceratohyal. The caproid arrangement deserves checking.

Various specialized or degenerate characters, such as only 13 branched caudal rays, indicate that the Zeiformes are not ancestral to the perciform assemblage, an ancestry which must be left to the Beryciformes.

Classification of this order follows Myers (1960).[1]

PARAZENIDAE

Branchiostegals. 7 in *Parazen.*
Reference. Mead (1957).
Material examined. None.

MACRUROCYTTIDAE (ZENIONTIDAE)

Branchiostegals. Zenion 8 and *Cyttula* 7. At least 5 judging from Fowler's figure of *Macrurocyttus.*
References. Fowler (1934), Jordan and Evermann (1898), Myers (1960), Weber and de Beaufort (1929).
Material examined. None.

ZEIDAE
Pl. 13

Branchiostegals. Vary from 7–8. *Zeus* 7 (8) (Starks stated 8 in text but figures only 7; other authors and my own observations show 7); *Cyttus* 7–8;

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[1] Modified to conform with Greenwood *et al.* (1966, Bull. Am. Mus. Nat. Hist. 131: 339–456).

Capromimus 7; *Parazen* 7. *Zeus faber* 7 with 0 epihyal and 7 ceratohyal, 4 external and 3 ventral, all acinaciform, the second to fifth having an anterior basal percopsid projection. *Capromimus abbreviatus* 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 on the ventral face of the hyoid arch, all acinaciform. *Cyttus novaezeelandiae* 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 ventral, all acinaciform.

Hyoid arch. In *Zeus* and *Capromimus* consists of interhyal, deep epihyal and ceratohyal, and two hypohyals. In *Zeus* the epihyal and ceratohyal have interdigitating prongs (an incipient suture) extending towards one another, but not in contact. *Zeus* with oval foramen in centre of ceratohyal; *Capromimus* with large foramen lacking dorsal border. In both, the fifth and sixth branchiostegals insert in notches on the lower border of the ceratohyal.

References. Fowler (1936), Mead (1957), Myers (1960), Starks (1898).

Material examined. Zeus faber, alizarin specimen, NMC62-144 & S, South Africa; alcoholic specimen, BC57-58, England; *Cyttus novaezeelandiae*, alcoholic specimen, BC56-269, Cook Strait, New Zealand; *Capromimus abbreviatus*, alizarin specimen, NMC62-245, New Zealand (erroneously reported as *Neocyttus gibbosus* in McAllister, 1964).

OREOSOMATIDAE

Branchiostegals. Allocyttus 7, *Xenocyttus* 7, *Oreosoma* 7.

References. Abe (1957*a*), Johnson and Hajny (1952), Jordan and Evermann (1898), Myers (1960).

Material examined. None.

GRAMICOLEPIDIDAE (GRAMMICOLEPIDAE)

Branchiostegals. 7 in *Grammicolepis* and *Xenolepidichthys*, all on the ceratohyal with 4 external and 3 ventral.

References. Goode and Bean (1896), Myers (1937).

Material examined. None.

CAPROIDAE (ANTIGONIIDAE)

Branchiostegals. Vary from 5–6. *Antigonia* 6, *Capros* 5, *Crassispinus* 6. *Antigonia rubescens* 6 with 4 epihyal and 2 ceratohyal.

Hyoid arch. In *Antigonia* consists of interhyal, deep epihyal, ceratohyal, and two hypohyals. The ceratohyal is pierced by a large foramen near its upper edge.

References. Berry (1959*a*), Fowler (1936), Goode and Bean (1896), Maul (1948), Starks (1902).

Material examined. None.

†PALAEOCENTRONOTIDAE

Branchiostegals. †*Palaeocentronotos boeggildi* 6 acinaciform present.

Reference. Kuhne (1941).

Material examined. None.

Order SYNGNATHIFORMES (AULOSTOMIFORMES)
Pl. 13

Branchiostegals 1–5 with 0–4 epihyal and 0–3 ceratohyal, 1–4 external and 0–1 interhyal, slender acinaciform or filiform. Interhyal (except *Fistularia*), epihyal, ceratohyal, and one or two hypohyals present. Epihyal and ceratohyal usually sutured together; arch modified in different fashion in each group. Branchiostegals often inserting under a lateral ridge on the ceratohyal. Lower hypohyal large, V-shaped, and usually receiving a wedge-shaped projection from the ceratohyal. Opercular bones complete and entire, without spines. Gill membranes separate or joined to the isthmus. Lower Oligocene to present. Six living families.

The Gasterosteiformes and Syngnathiformes (of Berg) have been variously associated in one order or in two adjacent orders by many authors such as Boulenger (1904), Berg (1947), Starks (1902*a*), and Bailey (1960) under such names as Thoracostei, Catosteomi, Hemibranchii, Gasterosteiformes, and Syngnathiformes. Regan (1929) included them all in the Solenichthyes, except for the Gasterosteidae and Aulorhynchidae which he placed in the Scleroparei. Bertin and Arambourg (1958) expanded Berg's classification and placed them all in three adjacent orders, Gasterosteiformes, Aulostomiformes, and Syngnathiformes. Gosline (1963*a*) questionably derives the Syngnathiformes and Gasterosteiformes from the Percopsiformes. Jungerson (1908, 1910), Starks (1902*a*), and Gregory (1933) have studied aspects of their osteology.

The Gasterosteiformes and Syngnathiformes have some obvious similarities, such as a long snout with a small and vertical mouth and pelvic fins which are abdominal or subthoracic. However, there are many fundamental differences between the groups. Gosline (1961) states that the syngnathiform jaws differ widely from the gasterosteiform jaws. Although the snouts are elongate in the two groups they are roofed differently, the frontals roofing the snout in the Gasterosteiformes but not in the Syngnathiformes. The soft pelvic rays number 1–4 in the Gasterosteiformes and 3–6 in the Syngnathiformes (or absent in Syngnathidae). The Gasterosteiformes possess ribs and parietals, unlike the Syngnathiformes. The construction of the hyoid arch is normal in the Gasterosteiformes but considerably modified in the Syngnathiformes; the hyoid arch does not project through the isthmus to form a knob in the Gasterosteiformes as it usually does in the Syngnathiformes. The Gasterosteiformes have a keel on the caudal peduncle, and the Syngnathiformes do not. The pelvics lie under the middle of the pectoral fin in the Gasterosteiformes but behind this point in the Syngnathiformes. The dorsal and anal fin rays are branched in the Gasterosteiformes and unbranched in the Syngnathiformes. The Gasterosteiformes are further united by the following breeding characteristics: the building of a nest of vegetation cemented together with kidney secretions; the guarding of the nest; the development of red or black colour in the breeding male of several of the genera.

The Gasterosteiformes are derivable from the Perciformes. The numerous pelvic fin rays and dorsal spines and other characters necessitate derivation of the Syngnathiformes from subperciforms, such as the Beryciformes or the Zeiformes.

Judging by the pelvic and dorsal fins and the number of branchiostegals, the Macrorhamphosidae and Solenostomidae appear to be the most primitive and the syngnathids the most advanced. The families are all quite highly specialized in their own directions, however, and none can easily be envisaged as ancestral to the others. Some of the Zeiformes, such as *Antigonia* or *Capromimus*, would appear to be close to the ancestors of the Syngnathiformes.

SOLENOSTOMIDAE

Branchiostegals. One branched filiform branchiostegal which curves up behind the operculum. This branchiostegal appears to have resulted from the fusion of two branchiostegals, one rising from the epihyal and one from the lower surface of the ceratohyal. Basally they are closely approximated and presumably fused, then for a short distance they are united by a bony membrane. Whereas the filiform shape of the branchiostegals is similar to that in Syngnathidae their insertion is different. Although the upper branchiostegal in *Aulostomus* and in *Fistularia* is also branched, it appears to be a result of one branchiostegal splitting rather than of two fusing; the shape also differs from that of *Solenostoma* in that the branchiostegals are distinctly acinaciform.

Hyoid arch. Consists of an interhyal, epihyal, ceratohyal, and two hypohyals. The interhyal is wedge-shaped with the broad end angled up and slightly enlarged. Its position is unusual, lying on the external face of the epihyal and ceratohyal. Neither the epihyal nor the ceratohyal sends prongs towards the other although the end of the ceratohyal is notched as if to receive a prong. The epihyal is only a fifth of the length of the ceratohyal. The two hypohyals send a wing posteriorly which extends nearly halfway along the mesial surface of the ceratohyal. The lower hypohyal lies anteriorly just beyond the ceratohyal; the upper one lies above the anterior end of the ceratohyal. The specialized hyoid arch of the Solenostomidae is quite unlike the specialized hyoid arch of the other three families.

References. Jungerson (1910), Weber and de Beaufort (1922).

Material examined. None.

MACRORHAMPHOSIDAE

Branchiostegals. Vary from 4–5. *Centriscops lilliei* 5 with 4 close together on the upper end of the ceratohyal, the fifth free in the membrane, all slender and acinaciform.

Hyoid arch. In *Centriscops* consists of a small oval interhyal imbedded in the reduced epihyal, a large triangular ceratohyal which extends into the large V-shaped lower hypohyal, and an upper hypohyal which lies above the posterior half of the ceratohyal. The elements are so closely adjoined that they are very difficult to discern.

References. Fowler (1936), Jordan and Evermann (1896), Weber and de Beaufort (1922).

Material examined. Centriscops lilliei, BC56-272, Cook Strait, New Zealand; hyoid arch and branchiostegals of one side dissected out, cleared, and stained with alizarin.

CENTRISCIDAE (AMPHISILIDAE)

Branchiostegals. Vary from 3–5. *Centriscus scutatus* 4 slender acinaciform branchiostegals, curving up around to middle of gill cover.

Hyoid arch. Consists of a round interhyal imbedded in upper end of arch, a small ventral epihyal, a large ceratohyal which sends a triangular prong into the large V-shaped lower hypohyal, and a small upper hypohyal above the end of the ceratohyal.

References. Chevey (1932), Danilchenko (1960), Day (1875), Jungerson (1910), Weber and de Beaufort (1922).

Material examined. Centriscus scutatus, alcoholic specimen, BC59-574, Bangkok.

FISTULARIIDAE

Branchiostegals. 5 in *Fistularia petimba* with 2–3 epihyal and 2–3 ceratohyal, all on the external face except the lowest which is on the internal face of the hyoid arch. All acinaciform and almost rectilinear. The uppermost forks once close to the expanded base. This fork is interpreted as the branching of a single branchiostegal (rather than a fusion of two) because there is no trace of fusion in the base and because there is the normal acanthopterygian complement of four on the external face of the hyoid arch. (If a fusion had taken place, one would expect only three branchiostegals on the external face.) Several authors give a count of 5–7 for this family. However, those authors who have made anatomical studies and this author are in agreement that the number is 5.

Hyoid arch. In *Fistularia* the epihyal sends a long wedge into the V-shaped ceratohyal, the lower hypohyal projects into the dorso-mesial face of the ceratohyal, and the upper hypohyal is small and lying above the lower hypohyal. Jungerson considered the absence of an interhyal to be caused by its fusion with the epihyal. Examination of the end of the epihyal in his figures leads me to deduce rather that the interhyal has been lost and the epihyal has elongated to make up for its absence.

References. Day (1875), Fowler (1936), Jordan and Evermann (1896), Jungerson (1910), Meek and Hildebrand (1923), Weber and de Beaufort (1922).

Material examined. Fistularia sp., skeletal specimen, USNM 26094, West Indies; *Fistularia petimba,* one alizarin plus two alcoholic specimens, BC57-79, Acapulco, Mexico.

AULOSTOMIDAE

Branchiostegals. 4 in *Aulostomus maculatus* and *A. chinensis. A. coloratum* 4, all on the outer face of the epihyal, the uppermost stoutest and terminally divided into filaments.

Hyoid arch. In *Aulostomus maculatus* interhyal triangular with broad end uppermost; epihyal sending a broad wedge into the V-shaped ceratohyal. Lower hypohyal sends a projection along the lower face of the ceratohyal. Upper hypohyal lies above and behind anterior end of the lower hypohyal.

References. Fowler (1936), Jordan and Evermann (1896), Jungerson (1910), Weber and de Beaufort (1922), Wheeler (1955).
Material examined. Aulostomus chinensis, alcoholic specimen, BC54-87, Hawaii.

SYNGNATHIDAE
Pl. 13

Branchiostegals. Vary from 1–3. *Syngnathus* 2–3, *Siphostoma* 2, *Hippocampus* 2, *Phyllopteryx* 2, and *Nerophis* 1. In *Syngnathus fuscus* two filiform ones emerge from under a small lateral projection on the external face of the ceratohyal and curl up around to the posterodorsal corner of the operculum (much as in Anguilliformes). The single branchiostegal of *Nerophis* is branched; probably it represents two branchiostegals fused basally. In *Hippocampus hilonis* two emerge from the external face of the ceratohyal. In *Siphostoma typhle* two filiform branchiostegals emerge from under a projection on the lateral face of the ceratohyal.
Hyoid arch. In *Syngnathus* and *Siphostoma* interhyal a round knob imbedded in the epihyal. Ceratohyal large with a small ventrally directed ridge terminating in a projection which hangs over the base of the branchiostegals; extends as a wedge into the lower V-shaped hypohyal. Upper hypohyal (absent in *Nerophis*) present in *Siphostoma, Hippocampus*, and *Syngnathus* and situated behind and above the anterior end of the hypohyal. Through comparison with *Centriscops* I was able to see that the interhyal of Jungerson (1910) consisted of the interhyal embedded in the epihyal. Thus the enigma of the apparent absence of an epihyal in Syngnathidae was solved. The hyoid arch makes a characteristic bulge on the underside of the head.
References. Jungerson (1910), Smitt (1895), Weber and de Beaufort (1922).
Material examined. Hippocampus hilonis, alizarin specimen, BC59-307, Vancouver Public Aquarium; *Syngnathus fuscus*, alizarin specimen, NMC61-172, Halifax, Nova Scotia; *S. griseolineata*, alizarin specimen, NMC61-98-S, Point Gravina, Alaska.

Order **OPHIDIIFORMES**, new order
Pl. 13

Branchiostegals (5) 6–9 (10) with 2 epihyal and 5–6 ceratohyal, 4 external and 3–4 ventral, all acinaciform, the middle ones often with anterior projections at the base. Interhyal, epihyal, ceratohyal, and two hypohyals present. The epihyal and the ceratohyal may be sutured together. Ceratohyal with projection under the hypohyals. Ceratohyal without foramen. Opercular bones complete, opercular spines 0–3. Gill membranes separate, narrowly attached to isthmus, or united and free from the isthmus. Four families. Fossils from the Palaeocene or Eocene to recent. Figure 1 shows the percopsid projection.

Gill (1884) included the Gadiformes, Ophidiiformes, Ateleopiformes, Zoarcidae, and several other percoids and blennioids in his order Jugulares. According to Garman (1899) the families Zoarcidae, Ophidiidae, and Brotulidae are closely related to the Gadidae and Macrouridae and belong in the order Anacanthini. Hubbs (1920) considered the Ophidiidae to be members of the Acanthopterygii. Goodrich (1909) considered the ophidioids allied to the Zoarcidae, and Boulenger (1910) considered ophidioids as degraded blenniids, not related to the cods. Gregory (1933) felt that evidence was insufficient to set aside the many signs of relationship between the anacanths and the blennies and ophidiids. Jordan put the ophidioids in his Jugulares, far from the cods. Regan (1912) placed them as the division Ophidiiformes in the suborder Blennioidea, and Berg (1947) placed them in their own suborder following the Blennioidei. Gosline (1953) indicated that *Dinematichthys* had a typically percoid caudal skeleton with 15 branched rays and (1961) that the basic pattern of the caudal skeleton of Beryciformes, Zeiformes, and Perciformes is similar. Rosen (1962) has suggested that the Ophidioidei, Gadiformes, Percopsiformes, and Amblyopsiformes form a phyletic assemblage. Gosline (1963*a*) believed that there is a close relationship between the percopsiforms and the amblyopsoids and that the percopsiforms share a common ancestry with the gadiforms. Freihofer (1963) considered the patterns of the ramus lateralis accessorius in Gadiformes, Ophidiidae, Brotulidae, and Zoarcidae to be basically alike, but unlike those of (other) blennioids.

The number, arrangement, and form of the branchiostegals of the Ophidiiformes, the suturing of the epihyal and ceratohyal, the opercular spines of some genera, the protusible upper jaw, and the caudal skeleton are all definite evidence that the Ophidiiformes are acanthopterygian fishes.

Several features differentiate the Ophidiiformes from the Perciformes. The Ophidiiformes differ radically from the percomorphs in the pectoral-pelvic branch of the ramus lateralis accessorius (Freihofer, 1963). The Ophidiiformes have a higher range of branchiostegals, usually 7–9, whereas the Perciformes usually have 4–7. The Ophidiiformes lack spiny rays in the fins, unlike Perciformes. These characters indicate that the Ophidiiformes are distinct from the Perciformes. The high number of branchiostegals in the Ophidiiformes and the evident affinities of the Ophidiiformes to the Gadiformes indicate that the Ophidiiformes are more primitive than the Perciformes.

The Ateleopiformes and Gadiformes are close to the Ophidiiformes (as will be shown below). Yet neither of these two orders can have given rise to the Ophidiiformes. The Ateleopiformes are very degenerate, lacking such structures as the basisphenoid, pterosphenoid, epiotic, opisthotic gas bladder, and scales which are present in the Ophidiiformes. The Gadiformes differ from the Ophidiiformes in having more numerous pelvic rays, the first two vertebrae long and with sessile epipleurals, the front of anterior centrum concave (instead of convex), no supramaxillary bone, the pelvic bones posterior to clavicular symphysis, no opercular spines, a mental barbel, two or three dorsal fins, no ceratohyal prong extending under the hypohyals. Thus the Gadiformes are distinct from the Ophidiiformes and cannot be immediately ancestral to them. This leaves only the Beryciformes as possible ancestors to the Ophidiiformes; the form of the branchiostegal bases would agree with this derivation, as well as branchiostegal number and arrangement (*see* next paragraph for sources of above data).

The Ophidiiformes do show many characters in common with the Ateleopiformes and Gadiformes as indicated by the following list (many not yet verifiable for the Ateleopiformes): large otoliths, males often sound producing and parapophyses broadened for gas bladder support; usually percopsid projection on fourth branchiostegal (except Ateleopiformes); vertical fin rays more numerous than one per vertebra (unlike Blennioidei); absence of orbitosphenoid and basisphenoid; fin spines absent (except possibly a single dorsal spine in some); pelvics thoracic to mental with one ray elongate and probably sensory; olfactory nerves not passing through orbits (except Gadoidei); scales cycloid (except Macrouroidei); opisthotic separating exoccipital and prootic; lower arm of operculum invading the suboperculum obliquely and suboperculum forming much of the border of the gill cover; upper jaw at least slightly protractile; branchiostegals usually 7–9; two hypohyals; hyomandibular broad; a supramaxillary (except Gadiformes); vertebrae numerous (about 45–89); caudal skeleton reduced and simplified to one or two plates (data from Clothier, 1950; Hotta, 1961; Regan, 1903; Gosline, 1953; Berg, 1947; Gregory, 1933).

From the above data it may be seen that the Ophidiiformes form a distinct order, yet they show affinities to the Ateleopiformes and Gadiformes (and ancestor-wise to the Beryciformes). Rosen (1962) has indicated that the Percopsiformes (and his Amblyopsiformes) also show affinities to this assemblage. Of the above characters they share the lack of an orbitosphenoid and basisphenoid; pelvics thoracic; opisthotic separating exoccipital and prootic (*see* Rosen's figures); hyomandibular broad; suboperculum forms most of posterior border of gill cover; two hypohyals; caudal fin reduced. They differ in having fewer vertebrae (27–36); in having a more normal caudal fin with up to 17 branched rays; in having a beryciform foramen; in having a short anal fin; and in lacking a protrusible upper jaw. It is concluded that they are related to the Ophidiiformes, Gadiformes, and Ateleopiformes but that they separated from them at an early stage.

For the sake of completeness the Gobioidei, another group with possible affinities to the Percopsiformes, may be mentioned here. The following features suggest relationship between the Gobioidei and the Percopsiformes: the opisthotics (when present) are between the exoccipitals and prootics (Gosline, 1955; Regan, 1911*d*); the operculum primitively bears two close spines (e.g., *Kraemeria*, *Typhlichthys*); the caudal skeletons of *Ptereleotris* and *Amblyopsis* are similar to one another in having two hypural plates with a small splint above and below and in having a plate-like ossicle in front of the upper splint (the goby differs by fusion of the upper hypural with the adjacent centrum); there is an interspace between the preoperculum and the symplectic (Gosline, 1955; Rosen, 1962); the gobioid scales bear some resemblance to those of percopsiforms (Cockerell, 1913); a broad parasphenoid and hyomandibular and similar gill rakers are present in *Eleotris* and Percopsiformes; the rows of neuromasts on the head in gobioids are similar to those of percopsiforms (although gobies examined lack the sublabial row); the branchiostegal number and arrangement of gobioids are similar to Percopsiformes. Cockerell (1913) notes of the percopsid scale that the form of the apical region, with the nucleus very far apiad and the single row of sharp teeth, reminds one of *Gobius* and its allies, although in Gobiidae the basal radii are very well formed and numerous. The gobioids differ from the percopsiforms by the lack of parietal bones, by the broad junction of the gill membranes with the isthmus, by the lack of a beryciform foramen in the ceratohyal, and by the lack of a frenum. The suggestion of relationship is preliminary and requires further investigation to determine if the similarities are parallelisms or whether they denote relationship. For the moment the Gobioidei are left in the Perciformes.

Recently doubt has been cast on the distinctness of the Brotulidae and the Ophidiidae. According to Norman their gill membranes are different. But the number of branchiostegals is almost the same (Ophidiidae 7–9 (10) and Brotulidae (5,6) 7–9). The families are here provisionally left separate.

OPHIDIIDAE

Pl. 13

Branchiostegals. Vary from 7–9 (10). *Brotuloides* 7, *Genypterus* 7, *Lepophidium* 7, *Ophidion* 7–10, *Otophidium* 7, *Parophidion* 7, *Raneya* 7, *Xylacyba* 8. *Genypterus capensis* 7 with 2 epihyal and 5 ceratohyal, 4 external and 3 ventral, all acinaciform, the middle 5 with anterior projections at the base. *Otophidium marginatum* 7, the upper scimitar-shaped; *Otophidium taylori* 7 with 2 epihyal and 5 ceratohyal, 4 external and 3 ventral, upper scimitar-shaped, broad mesially.

Hyoid arch. In *Genypterus* and *Otophidium* consists of interhyal, epihyal, ceratohyal, and two hypohyals. The epihyal and ceratohyal sutured internally and externally. Beryciform foramen lacking.

References. de Beaufort and Chapman (1951), Böhlke and Robins (1959), Cohen (1961), Fowler (1936), Garman (1899), Harry (1951*a*), Robins (1961).

Material examined. Otophidium marginatum, alcoholic specimen, USNM 131497, Cape Hatteras, Florida; *O. welshi,* alcoholic specimen, USNM 102178, off Virginia Capes; *O. taylori,* alcoholic specimen, BC61-200, Santa Monica Bay, California; *Genypterus capensis,* alizarin specimen, NMC62-143 & S, South Africa.

BROTULIDAE

Pl. 13

Branchiostegals. Vary from (5,6)7–9. *Alcockia* 8, *Barathrites* 6, *Barathrodemus* 8, *Bassozetus* 8, *Bathronus* 5, *Brotula* 8, *Cattaetyx* 8–9, *Celema* 8, *Dicrolene* 8, *Dinematichthys* 6–7, *Diplocanthopoma* 8, *Echelybrotula* 7, *Eretichthys* 8, *Glyptophidium* 8, *Holomycteronus* 8, *Hypleuron* 8, *Lamprogrammus* 8, *Leucicorus* 8, *Mastigopterus* 8, *Monomeropus* 8, *Monomitopus* 8, *Neobythites* 8, *Oligopus* 8, *Parabrotula* 5 or 6, *Porogadus* 8, *Pseudonus* 8, *Pycnocraspedon* 8, *Sciadonus* 7, *Vulcanus* 8,[1] *Xenobythites* 8. *Brotula multibarbata* 8 with 2 epihyal and 6 ceratohyal, 4 external and 4 on the ventral face of the hyoid arch, all acinaciform. *Ogilbia* sp. 7 with 2 epihyal and 5 ceratohyal, 4 external and 3 in notches on the ventral face, all acinaciform, the middle 5 with anterior projections on their bases.

Hyoid arch. In *Ogilbia* consists of interhyal, epihyal, ceratohyal, and two

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[1] *Vulcanus* is a synonym of *Luciobrotula* according to Cohen (1964), Bull. Mar. Sci., Gulf Caribb. 14 (3): 387.

hypohyals. The latter nearly sutured together; no ceratohyal foramen. In *Dicrolene* (Gregory, 1933, Fig. 256) ceratohyal bowed downward.
References. de Beaufort and Chapman (1951), Fowler (1936), Garman (1899), Gosline (1953), Günther (1887), Norman (MS.).
Material examined. Brotula multibarbata, alcoholic specimen, USNM 167354, Gilbert Islands; *Ogilbia* sp., alizarin specimen, NMC62-217 & S, Las Tres Marias Islands, Mexico.

PYRAMODONTIDAE

Branchiostegals. 7 in *Pyramodon. Snyderidia* 7 with 2 epihyal and 5 ceratohyal.
References. de Beaufort and Chapman (1951), Gosline (1960*a*), J.L.B. Smith (1955).
Material examined. None.

CARAPIDAE (FIERASFERIDAE)

Branchiostegals. Vary from 6–7. *Carapus* 7, *Onuxodon* 7, *Echiodon* 7, *Encheliophis* 6–7.
References. Arnold (1956), de Beaufort and Chapman (1951), Bonham (1960), Fowler (1936), Smith, J. L. B. (1955*a*), Smitt (1895).
Material examined. Encheliophis (*Jordanicus*) *gracilis*, alcoholic specimen, USNM 65884, Tahiti.

Order ATELEOPIFORMES

Pl. 13

Branchiostegals 7–9, with 3–4 epihyal and 4 ceratohyal, 4 external and 3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present and separated by cartilage. Epihyal and ceratohyal not sutured. No ceratohyal projection under hypohyals. Ceratohyal without foramen. Opercular bones complete and entire. Gill membranes separate. A single family. Fossils unknown.

Goode and Bean (1896) and Boulenger (1904) placed the Ateleopidae next to the Ophidiidae. Radcliffe (1913) placed the Ateleopiformes in the macrouroids. Regan (1929) put the Ateleopidae in a separate suborder under the Iniomi; Bertin and Arambourg (1958) placed them next to the Miripinnatoidei and Myctophoidei in the Clupeiformes. Berg (1947) placed them in their own order, Ateleopiformes, following the Myctophiformes. Bertelsen and Marshall (1958) considered the Miripinnati very close to the Ateleopidae. Walters (1962, unpublished paper presented at ASIH meetings) considered them related to the Miripinnati. Bertelsen and Marshall (1956) suggested that the Miripinnati were closer to the Chondrobrachii (=Ateleopiformes) than any other preberycomorph order considered.

The bordering of the upper jaw solely by the premaxilla separates the Ateleopidae from the Clupeiformes and lower orders. A protrusible upper jaw is very rarely found in malacopterygian fishes. The Ateleopidae have jugular pelvics, a character unknown in the malacopterygians. The arrangement and the form of the branchiostegals are acanthopterygian, the number is primitive acanthopterygian. These three strong characters would therefore place the Ateleopidae amongst the acanthopterygians. Doubtless the absence of spines has been partly responsible for the allocation amongst malacopterygians. However, the long first dorsal ray of a specimen of *Ijimaia antillarum* (under a microscope but without dissection or staining) appeared to lack annulae and appeared to be a flexible spine. The lack of an acanthopterygian suture between the epihyal and ceratohyal may be related to the reduction of ossification in this deep-sea group.

Relationship to the Mirapinniformes has been suggested. But they have 17 principal caudal rays and 4–10 pelvic rays whereas the Ateleopidae have 14 or fewer caudal rays (14 in *Ijimaia* and 10 in *Ateleopus*) and 1–3 pelvic rays. More detailed osteological studies are needed.

To what other group of acanthopterygians might the Ateleopidae be related? The presence of a supramaxillary restricts derivation to the Perciformes or sub-Perciformes. Of these, the only orders having as many branchiostegals and far forward pelvics are the Ophidiiformes and the Beryciformes. The number of pelvic rays, caudal rays, and vertebrae; the position of the pelvics; and the absence of a basisphenoid in the Ateleopidae all agree with the Ophidiiformes rather than the Beryciformes. Derivation of the Ateleopidae from the Ophidiiformes is indicated. Differences between the two orders are mainly those of reduction. The ateleopids have only one pelvic radial and lack the scales, opisthotics, pterosphenoids, and epiotics found in Ophidiiformes. The shorter dorsal of the Ateleopidae is difficult to interpret; it may represent the retention of a more primitive condition or a secondary shortening. Further resemblances between the Ateleopidae, ophidiiforms, and gadiforms are discussed under the Ophidiiformes.

ATELEOPIDAE (GUENTHERIDAE)

Pl. 13

Branchiostegals. Vary from 7–9. *Ateleopus natalensis* 7 with 3 epihyal and 4 ceratohyal, 4 external and 3 on the ventral face of the hyoid arch, all acinaciform (the branchiostegals lying in the gap between the epihyal and ceratohyal are distributed in the formula as they would be if the epihyal and ceratohyal met). *A. indicus* 7–8 with 3–4 epihyal and 4 ceratohyal; *A. natalensis* 7 with 3 epihyal and 4 ceratohyal; *A japonicus* 8 (9 specimens) or 9 (2 specimens); *Ijimaia plicatella* 8 (2 specimens); *I. fowleri* 7 (1); *I. loppei* 7 (2); *I. antillarum* 7 (2 specimens) with 4 on external epihyal and 3 on ventral ceratohyal.

Hyoid arch. In *Ateleopus natalensis* consists of interhyal, epihyal, ceratohyal, and two hypohyals. The hypohyals are separated by cartilage. There is a gap between the epihyal and ceratohyal.

References. Alcock (1891), Bertelsen and Marshall (1956), Günther (1887), Misra (1953), Rivero (1935), Weber and de Beaufort (1929).

Material examined. Ateleopus natalensis, hyoid arch and rays dissected out, SU 31358, Durham, Natal; *Ijimaia antillarum*, alcoholic specimen, USNM 157993, south of Mobile, Alabama.

Order **GADIFORMES (MACROURIFORMES)**

Pls. 13, 14

Branchiostegals (5) 6–8 with 0–1 epihyal and 5–8 ceratohyal, 4 external and 3–4 on the ventral face of the hyoid arch, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present. Epihyal and ceratohyal usually connected on their internal faces by a suture (except in Moridae); the hypohyals and ceratohyal separate. Without ceratohyal projection under hypohyals. Ceratohyal without beryciform foramen. Opercular bones complete and entire. Gill membranes separate, united and free from, or joined to isthmus. Three suborders with 6 families. Lower Tertiary (Palaeocene) to present.

Berg (1947) regarded the Gadiformes as a lowly organized order derived from forms allied to the Pachycormidae, probably at the end of the Cretaceous. Regan (1910) considered the cods much more generalized than the ophidioids, near which they have been placed by some authors, and thought that they were perhaps derived from some generalized myctophoid stock such as the Aulopidae. Hubbs (1920) regarded *Corphaenoides* as having a typically acanthopterygian branchiostegal apparatus. Gregory (1933) believed that many features suggested relationship to various percomorphs and considered that the opercular region differed most widely from the *Aulopus* type. According to Gosline (1961) the protrusible upper jaw of Gadiformes and Macrouriformes seemed essentially of perciform type. The retractores arcuum branchialium reported in Gadiformes by Holstvoogd (1963) is another acanthopterygian character.

The double hypohyal, sutured epihyal and ceratohyal, and acinaciform branchiostegals provide arguments against Berg's derivation of the Gadiformes from the Pachycormiformes and suggest derivation from higher forms. The number, arrangement, and form of the branchiostegals are those of primitive acanthopterygians, and the suture between the epihyal and ceratohyal strengthens acanthopterygian placement. Other characters agreeing with this position are the protrusible upper jaw, the dorsal fin spine in the macrouroids, the anterior pelvics, the bordering of the upper jaw solely by the premaxillary, the physoclistic gas bladder, the retractores arcuum branchialium, the absence of intermuscular bones, and the absence of an orbitosphenoid.

Two characters have offered difficulty in the placement of the Gadiformes, the numerous pelvic rays (5–17) and the absence of fin spines (except the first dorsal ray of macrouroids and possibly the first dorsal ray of *Merluccius*). However, none of the Malacopterygii or Holostei have as many as 17 pelvic rays (except Cypriniformes which cannot of course be ancestral). Therefore, the pelvic ray count of up to 17 is not a primitive condition but represents a secondary multiplication (as in some Pleuronectiformes where the pelvic rays have secondarily multiplied to 13). However, a sufficient number of the more primitive members do have a pelvic count of seven to suggest that this is close to the original number of the order. This number would suggest that the Gadiformes are more primitive than the Perciformes.

The pelvic ray count of 7 and the branchiostegal number of 5–8 suggest derivation from the Beryciformes or Zeiformes. Osteological characters of the

Gadiformes make a derivation from the Beryciformes more likely. As is discussed under the Ophidiiformes, it is likely that the Gadiformes and Ophidiiformes arose from a single offshoot of the Beryciformes.

Suborder **Gadoidei**

MORIDAE (TRIPTEROPHYCIDAE)

Pl. 14

Branchiostegals. Vary from (6) 7(8). *Laemonema* 7, *Physiculus* 7, *Gadella* 7, *Mora* 7, *Halogyreus* 7, *Brosmiculus* 6, *Lepidion* 7(8), *Antimora* 7, *Tripterophycis* 7, *Gargilius* 7. Günther (1887) reported *Melanonus* with 5, but Koefoed (1953), Gregory (1933), Maul (1952), and Beebe (1932) all report 7 and it seems likely Günther either was in error or had an abnormal specimen. *Antimora rostrata* 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 ventral, all acinaciform; the fourth branchiostegal with percopsid projection.

Hyoid arch. In *Antimora* consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal separated by cartilage.

References. Beebe (1932), Böhlke and Mead (1951), Fowler (1936), Garman (1899), Günther (1887), Koefoed (1953), Maul (1952), Weber and de Beaufort (1929), Whitley (1948).

Material examined. Antimora rostrata, alizarin specimen, NMC62-118 & S, Grand Banks, Newfoundland.

BREGMACEROTIDAE

Branchiostegals. 7 in *Auchenoceros* and *Bregmaceros. Auchenoceros punctatus* 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 ventral, all acinaciform.

Hyoid arch. In *Auchenoceros* consists of interhyal, epihyal, ceratohyal, and two hypohyals. Ceratohyal bent downwards as in some ophidiiforms. Epihyal and ceratohyal sutured together.

References. Day (1875), Garman (1899), Weber and de Beaufort (1929).

Material examined. Auchenoceros punctatus, alizarin-stained dissection, BC56-281, Otago, New Zealand.

GADIDAE (MERLUCCIIDAE, RANICEPITIDAE)

Pl. 14

Branchiostegals. Varies from (6)7(8). *Lota* 7(8), †*Palaeogadus* 7, *Gadiculus* 7, *Gaidropsarus* 7, *Gadus* 7, *Pollachius* 7, *Merluccius* 7, *Molva* 7, *Melanogrammus* 7, *Phycis* 7, *Onus* (6)7, *Raniceps* 7, *Brosmius* 7. *Lota lota* 7–8 with 0 epihyal and 7–8 ceratohyal, 4 external, the next on the internal, and the anterior 2–3 on the ventral face of the hyoid arch, all acinaciform. *Raniceps* 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 internal. *Merluccius productus* 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 internal, all acinaciform, numbers 3 and 4 with anteriorly directed projections at the base. The fourth branchiostegal with percopsid projection. Marshall[1] removes *Macru-*

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[1] Marshall, N. B. 1966. The relationships of the anacanthine fishes, *Macruronus, Lyconus,* and *Steindachneria.* Copeia (2): 275–280, 3 figs.

ronus, *Lionurus*, *Steindachneria* (all with 7), and *Lyconodes* from the Macrouridae to the Merlucciidae (which is here included in the Gadidae).
Hyoid arch. In *Lota* consists of interhyal, epihyal, ceratohyal, and two hypohyals, the epihyal and ceratohyal sutured internally, the hypohyals not sutured. In *Merluccius* the epihyal and ceratohyal sutured internally, the ceratohyal angled downwards as in ophidiiforms.
References. Berg (1949), Danilchenko (1960), Fowler (1936), Gill (1891*a*), Jordan and Evermann (1898), Maul (1952), Smitt (1892).
Material examined. Lota lota, alizarin specimen, MNC60-453 & S, Aklavik, Northwest Territories; skeletal specimen, uncatalogued specimen, Inst. Fish., University of British Columbia, Squanga Lake, Yukon; *Merluccius productus*, skeletal specimen, Inst. Fish., University of British Columbia collection, California.

Suborder **Muraenolepoidei**

MURAENOLEPIDIDAE

Branchiostegals. Muraenolepis marmorata 5, the second one with an anterior basal process directed downwards.
Reference. Günther (1880).
Material examined. None.

Suborder **Macrouroidei**

MACROURIDAE (MACRURIDAE)

Pl. 13

Branchiostegals. Vary from 6–7(8). *Bathygadus* 6–7, *Cariburus* 6, *Cetonurus* 7, *Coelorinchus* 6, *Coryphaenoides* 6, *Cynomacrurus* 6, *Echinomacrurus* 7, *Grenurus* 7, *Hymenocephalus* 7, *Macrourus* 6–7(8), *Malacocephalus* 7, *Mataeocephalus* (6)7, *Odontomacrurus* 6, *Oxygadus* 6, *Phalacromarurus* 6–7, *Trachonurus* 7, *Trachyrinchus* 7, *Ventrifossa* (6)7. *Macrourus bairdii* 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 ventral, all acinaciform, the fourth with an anterior prong at the base (the percopsid projection, *see* fig. 2).
Hyoid arch. In *Macrourus* consists of interhyal, epihyal, ceratohyal, and two hypohyals. The epihyal and ceratohyal joined internally by a suture; the hypohyals separate except that the lower one sends a broad prong on the internal face of the ceratohyal.
References. Fowler (1936), Garman (1899), Gilbert and Hubbs (1916), Koefoed (1953), Maul (1951, 1952), Norman (MS.), Parr (1946), Smitt (1895), Weber and de Beaufort (1929).
Material examined. Macrourus bairdii, alizarin specimen, NMC62-115-S, Grand Banks, Newfoundland.

MACROROIDIDAE

Branchiostegals. 7 in *Squalogadus modificatus*.
References. Gilbert and Hubbs (1916), Radcliffe (1913).
Material examined. None.

Order PERCOPSIFORMES (AMBLYOPSIFORMES)

Pl. 14

Branchiostegals 6(7) with 1 epihyal and 5 ceratohyal, 4 on the lateral face and 2 on the ventral face of the hyoid arch, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present. Epihyal and ceratohyal sutured or with vestiges of sutures. Ceratohyal with or without a beryciform foramen. Opercular bones complete; operculum with none, one, or two spines. Gill membranes separate or joined far forward to isthmus. Eocene to present. Three families known.

According to Regan (1929) this is an isolated order without evident relationships except to the Isospondyli or primitive Iniomi. According to Hubbs (1920) the Percopsiformes have six branchiostegals exactly as in the Acanthopteri. According to Gosline (1961) the caudal skeleton is specialized and similar to that of the Cyprinodontiformes, but the pelvic structure and antorbital bone indicate a "lower" teleostean condition, the ensemble of characters suggesting that they are an offshoot of a primitive scopeliform or protoscopeliform. Bailey (1960) suggests that they are perhaps remotely related to the Beryciformes. Gosline (1963) indicates that the cyprinodontiforms are percopsiform derivatives and that the Percopsiformes share a common ancestry with the Gadiformes. Patterson (1964) suggests derivation from the Ctenothrissiformes.

The branchiostegal number, form, and arrangement; the suturing together of the epihyal and ceratohyal; the presence of spines in the fins; the ctenoid scales; the retractores arcuum branchialium; and the presence of opercular spines in some members all suggest that these are acanthopterygian fishes. The 16–17 branched caudal rays and numerous pelvic rays indicate that the Percopsiformes are more primitive than the Perciformes and the Zeiformes but less primitive than the Beryciformes. The Beryciformes or the Ctenothrissiformes indeed form the logical ancestors of the Percopsiformes. Confirmatory evidence of this is furnished by a foramen in the ceratohyal of *Percopsis*, by the one or two opercular spines (in Amblyopsidae and *Aphredoderus*), and by the lacrymal and preopercular spines of *Aphredoderus*. Rosen (1962) suggests affinity with the ophidioids and gadiforms; evidence for this is discussed under the Ophidiiformes. The evidence suggests origin on a common line, with perhaps the percopsiforms branching off earlier on the common line from the beryciforms. It was also pointed out under the Ophidiiformes that the gobioids may be related to the Percopsiformes.

Starks (1904) placed the Amblyopsidae together with the pikes and topminnows in his order Haplomi. Regan (1911*a*) detached the pikes and placed the cyprinodonts and amblyopsids as distinct suborders in a new order Microcyprini. This arrangement has been followed by Berg (1947). But differences began to accumulate between the two suborders since Regan erected them. Regan himself found several profound differences. Frost (1926) found that the otoliths of *Amblyopsis* showed no resemblance to those of other cyprinodontiforms. Woods and Inger (1957) added further distinguishing characters whilst revising the Amblyopsidae. Bertin and Arambourg (1958) erected a new order for the reception of Amblyopsidae. Gosline (1961) found differences between amblyopsoids and (other) cyprinodontiforms, and at the same time he indicated similarities in the caudal skeleton of amblyopsids and *Aphredoderus*. Gosline (1963*a*) reaffirmed the similarity between percopsiforms and amblyopsids. Rosen (1962) studied carefully the relationships of Amblyopsidae and found that they had been misplaced in the Cyprinodontiformes; he showed numerous osteological, myological, and functional similarities to *Aphredoderus*. He provisionally assigned the Amblyopsidae to a separate order adjacent to the Percopsiformes.

Evidence was found in this study to support the views of Gosline and Rosen. The Amblyopsidae were found to have two hypohyals and opercular spines unlike cyprinodontiforms but like percopsiforms. The hypohyals are sutured to the ceratohyal unlike the Cyprinodontiformes but like the Percopsiformes. Further, the sublabial, mandibular, and cephalic rows of neuromasts in aphredoderids and in percopsiforms show surprising resemblance (*see* and compare fine figures of Woods and Inger, 1957, and Moore and Burris, 1956). The first dorsal ray of a cleared and stained *Typhlichthys* appeared to be spinous, unlike the dorsal of Cyprinodontiformes but like that of Percopsiformes. In Amblyopsidae the opisthotic separates the exoccipital and prootic as in Percopsiformes. Rosen notes other similarities. These close similarities to the Percopsiformes as well as the differences shared with the Percopsiformes differentiating them from the related ophidiiforms, ateleopiforms, and gadiforms indicate to me that the Amblyopsidae belong in the order Percopsiformes. The differences between the Amblyopsidae and other Percopsiformes appear to be of about the same importance as those between Aphredoderidae and Percopsidae, thus Amblyopsidae and Aphredoderidae may be accommodated in the same order.

Suborder **Aphredoderoidei**

APHREDODERIDAE

Pl. 14

Branchiostegals. 6 in *Aphredoderus sayanus* with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform, the uppermost fairly broad mesially, almost crescentic; the lower two fitting into notches on the lower side of the ceratohyal; with percopsid projection at base of fourth.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal strongly sutured together, a suture also joining each hypohyal to the ceratohyal. Upper border of ceratohyal emarginated; a short arm projects over this evacuation from the posterior end of the ceratohyal. It may be interpreted as a beryciform foramen the upper border of which has been lost permitting it to open on the upper edge of the ceratohyal. This interpretation is strengthened by the finding of a small but normal beryciform foramen in Percopsidae and by the fact that the zeiform *Neocyttus* has similarly lost the dorsal border to its foramen (unlike *Zeus*).

References. Hubbs (1920), Jordan and Evermann (1896).

Material examined. Aphredoderus sayanus gibbosus, alizarin specimen, NMC62-72, North Branch of the Bad River, Michigan.

Suborder **Amblyopsoidei**

AMBLYOPSIDAE
Pl. 14

Branchiostegals. Typhlichthys subterraneous 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform. *Chologaster agassizi* 6 with 4 external and 2 ventral.

Hyoid arch. In *Typhlichthys* consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal sutured on dorsal internal face by two prongs. Hypohyals each send a prong towards the ceratohyal. No beryciform foramen.

References. Jordan and Evermann (1896), Rosen (1962), Woods and Inger (1957).

Material examined. Typhlichthys subterraneous, alizarin specimen, NMC58-5 & S, Mammoth Cave, Kentucky, August 1863; *Chologaster agassizi,* alcoholic specimen, NMC59-82, Kentucky.

Suborder **Percopsoidei**

PERCOPSIDAE

Branchiostegals. 6(7) in *Percopsis omiscomaycus* with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform, the fourth one with a percopsid projection at the base, the uppermost fairly broad mesially. *Columbia transmontana* 6 with 4 external and 2 ventral. In 50 specimens of *Percopsis omiscomaycus,* 48 were found with 6 and 2 with 7 branchiostegals. Percopsid projections present (*see* fig. 1).

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal separate or with 1–3 prongs extending towards one another. Prongs extending from lower hypohyal towards the ceratohyal, but not from the upper. A small beryciform foramen in the upper mesial ceratohyal, sometimes fused over. Upper hypohyal extends slightly over anterior end of the ceratohyal.

References. Hubbs (1920), Jordan and Evermann (1896).

Material examined. Percopsis omiscomaycus, alizarin specimen, NMC60-469-A, Lake Erie, Ontario; alizarin specimen, BC57-224, Fort Nelson, B.C.; 50 alcoholic specimens, BC57-362, Alberta.

Order **ATHERINIFORMES (BELONIFORMES, CYPRINODONTIFORMES, PHALLOSTETHIFORMES)**
Pl. 15

Branchiostegals 4–15 with 1–4 epihyal, 4–9 ceratohyal, and 0–3 hypohyal, 4(5) external and 1–2 ventral (except exocoetoids where all except 1 or 2 are external). Interhyal (except exocoetoids), epihyal, ceratohyal, and a lower and sometimes (atherinoids) an upper hypohyal. Epihyal and ceratohyal sutured. Opercular bones complete and entire. Gill membranes separate or united and free from the isthmus. Three suborders with eighteen families. Eocene to present.

See Rosen (1964) for the history and characterization of this group.

The exocoetoids differ from the other atheriniforms in their lack of an interhyal, in the external placement of their branchiostegals, and in the elevated number of branchiostegals. Despite the elevated number of branchiostegals they possess the suturally united epihyal and ceratohyal characteristic of acanthopterygians. The elevated number is probably a secondary feature. This feature is shared with the Echeneiformes, a group with which several other characteristics are shared (and which would bear closer investigation in this regard).

The atherinoids are distinguished from the other atheriniforms by the possession of two hypohyals.

The Tselfatoidei, placed by Bertin and Arambourg amongst the Beloniformes, have been shown to belong amongst the clupeiforms.

It is questionable whether a new ordinal name should have been erected for this group when three were 'available,' but perhaps the taxon requires a new label because it has been so greatly modified.

Suborder **Atherinoidei**

Superfamily ATHERINOIDEA

MELANOTAENIIDAE

Branchiostegals. 6 in *Pseudomugil* with 2 epihyal and 4 ceratohyal, 4 external and 2 ventral, all acinaciform, the upper four with ragged anterior edges.
Hyoid arch. Consists in *Melanotaenia* of epihyal, ceratohyal, and two hypohyals (interhyal not figured).
References. Rosen (1964), Whitley (1948).
Material examined. None.

ATHERINIDAE

Pl. 15

Branchiostegals. 6 in *Atherina, Hepsetia,* and *Menidia. Menidia menidia* 6 with 2 epihyal and 4 ceratohyal, 4 external and 2 internal, all acinaciform. Most authors give 5–6 as the range for the family.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal sutured dorsally; both hypohyals sutured to ceratohyal. Specimen of *Menidia menidia* examined did have the typical posterior expansion of the ceratohyal, unlike those of *M. beryllina* examined by Rosen.
References. Berg (1949), Day (1875), Fowler (1936), Weber and de Beaufort (1922).
Material examined. Menidia menidia, two alizarin specimens, NMC59-288, Prince Edward Island.

ISONIDAE

Branchiostegals. 6 in *Iso rhothophilus.*
References. Jordan and Starks (1901), Ogilby (1895), Rosen (1964).
Material examined. None.

Superfamily PHALLOSTETHOIDEA

PHALLOSTETHIDAE (NEOSTETHIDAE)

Branchiostegals. 5 in *Phenacostethus smithi*, *Gulaphallus mirabilis*, and *Neostethus siamensis*, all with 4 external and 1 ventral. *Neostethus siamensis* 1 epihyal and 4 ceratohyal, all acinaciform but uppermost broad in the middle and scimitar-like.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and one hypohyal, the lower. Epihyal and ceratohyal sutured together dorsally.
References. Bailey, R. J. (1936), Hubbs (1944), Myers (1928).
Material examined. Neostethus siamensis, alizarin specimen, uncatalogued, Inst. Fish., University of British Columbia.

Suborder **Cyprinodontoidei**

Superfamily ADRIANICHTHYOIDEA

ORYZIATIDAE

Branchiostegals. 6 in four specimens of *Oryzias latipes* with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform.
Hyoid arch. Includes epihyal and ceratohyal sutured together dorsally.
Reference. Rosen (1964).
Material examined. Oryzias latipes, four alizarin specimens, uncatalogued specimen of aquarium stock at Inst. Fish., University of British Columbia.

ADRIANICHTHYIDAE

Branchiostegals. 6–7 in *Xenopoecilus*, 5 in *Adrianichthys*. Rosen shows 6 in *X. sarasinorum* with 5 external and one free, one epihyal, 4 ceratohyal and one free.
Hyoid arch. Includes epihyal sutured dorsally to ceratohyal, a single ventral hypohyal; interhyal not figured.
References. Rosen (1964), Weber and de Beaufort (1922).
Material examined. None.

HORAICHTHYIDAE

Branchiostegals. 4 in *Horaichthys setnai.*
References. Kulkarni (1940), Rosen (1964).
Material examined. None.

Superfamily CYPRINODONTOIDEA

CYPRINODONTIDAE

Branchiostegals. Vary from 5–6(7). *Adinia* 5, *Aplocheilus* 5, *Cynolebias* 7, *Cyprinodon* 5–6, *Empetrichthys* 5, *Fundulus* 5–6, *Haplocheilus* 5–6, *Haplochilichthys* 5, *Jordanella* 5, *Lebias* 5, *Lucania* 6, *Orestias* 5, *Panchax* 5, *Pterolebias* 6, *Rivulus* 6, *Simpsonichthys* 6, *Zygonectes* 5(6). *Fundulus diaphanus* 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform.

Hyoid arch. In *Fundulus* interhyal, epihyal, ceratohyal, and the lower hypohyal present. Epihyal and ceratohyal sutured dorsally.
References. de Carvalho (1959), Eigenmann and Allen (1942), Garman (1895), Weber and de Beaufort (1922).
Material examined. Fundulus diaphanus, alizarin specimen, NMC62-77, Rideau River, Ontario.

GOODEIDAE

Branchiostegals. Vary from 4–5. *Goodea* 5, *Zoogeneticus* 4, *Characodon* 4, *Girardinichthys* 5, *Xenotoca* 5. *Goodea* sp. 5, the upper two fairly broad. *Xenotoca variata* 5 with 1 epihyal and 4 ceratohyal, 4 external and 1 internal, all acinaciform but upper ones broad mesially.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and the lower hypohyal in *Xenotoca*; epihyal and ceratohyal sutured together dorsally; hypohyal and ceratohyal separate.
References. Garman (1895), Hubbs (1932).
Material examined. Goodea sp., 2 alcoholic specimens, BC60-7, Chapala, Mexico; *Xenotoca variata*, alizarin specimen, NMC62-68, Rio de Aguas, Mexico.

JENYNSIIDAE

Branchiostegals. Jenynsia 5, hidden under gill cover.
References. Garman (1895), Myers (1931*a*).
Material examined. Jenynsia lineata, alcoholic specimen, USNM 84469, Buenos Aires, Argentina.

ANABLEPIDAE

Pl. 15

Branchiostegals. 6 in *Anableps. Anableps dovii* 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform but uppermost broad mesially.
Hyoid arch. Consists in *Anableps* of interhyal, epihyal, ceratohyal, and the lower hypohyal. Epihyal and ceratohyal joined by a dorsal suture. Hypohyal sutured ventrally to the ceratohyal.
Reference. Garman (1895).
Material examined. Anableps dovii, alizarin specimen, NMC62-71, Honduras.

POECILIIDAE (TOMEURIDAE)

Pl. 15

Branchiostegals. Vary from 5–6. *Poecilia* 5–6, *Tomeurus* 5, *Gambusia* 6, *Belonesox* 6, *Cnesterodon* 5, *Girardinus* (*Glaridodon* incl.) 5, *Xiphophorus* 5, *Heterandia* 5–6. *Poecilia viriosa* 5 with 1 epihyal and 4 ceratohyal, 4 external and 1 ventral, all acinaciform.
Hyoid arch. In *Poecilia* consists of interhyal, epihyal, ceratohyal, and the lower hypohyal; epihyal and ceratohyal sutured dorsally; hypohyal and ceratohyal separate.

Taxonomy. The genera of Rosen and Bailey are used herein.
References. Garman (1895), Gregory (1933), Jordan and Evermann (1896), Meek (1904), Meek and Hildebrand (1916), Rosen and Bailey (1959, 1963), Rosen and Kallman (1959).
Material examined. *Poecilia viriosa*, alizarin specimen, NMC59-181 & S, Los Llanos, Mexico; *Tomeurus gracilis*, alcoholic specimen, USNM 92977, British Guiana.

Suborder **Exocoetoidei**

Superfamily SCOMBERESOCOIDEA

†ROGENIIDAE, *incertae sedis*

Branchiostegals. No data available.
Reference. Jordan (1923).

†FORFICIDAE, *incertae sedis*

Branchiostegals. No data available.
Reference. Jordan (1923).

BELONIDAE

Pl. 15

Branchiostegals. Vary from 9–15 with 3 epihyal, 8 ceratohyal, and 0–1 hypohyal. *Belone* (including *Tylosurus* and *Ablennes*) 9–15. *Belone houttuyni* (formerly *marinus*) 11–12 with 3 epihyal, 8 ceratohyal, and 0–1 hypohyal, all on the external face of the arch except perhaps the lowest which may lie free. All laminar acinaciform, bending halfway up behind the gill cover. The bases of those inserting on the ceratohyal are expanded into an oval.
Hyoid arch. In *Belone* interhyal and dorsal hypohyal absent; epihyal and ceratohyal sutured and of even width. Hypohyal set into the lower part of the ceratohyal.
References. Day (1875), Mees (1962), Smitt (1892), Weber and de Beaufort (1922).
Material examined. *Belone houttuyni*, alizarin specimen, NMC62-127 & S, Florida; alizarin specimen, NMC62-73 & S, North Carolina.

SCOMBERESOCIDAE

Branchiostegals. Vary from 14–15. *Cololabis* 14–15, *Scomberesox* 14. *Cololabis saira* 14–15 with 3–4 epihyal, 8–9 ceratohyal, and 2–3 hypohyal, all on the external face of the hyoid arch, although the anteriormost may lie free in the gill membrane. Branchiostegals almost rectilinear, do not curve up behind gill cover; upper ones broad, laminar, pointed; lower ones attenuate.
Hyoid arch. Interhyal and upper hypohyal absent in *Cololabis*; epihyal and ceratohyal sutured; hypohyal inserts into ventral margin of ceratohyal.
References. Chapman (1943*a*), Smitt (1892).
Material examined. *Cololabis saira*, alizarin specimen, BC60-194, off Queen

Charlotte Islands, B.C.; alizarin specimen, NMC60-312, 620 miles west of Vancouver Island, B.C.

Superfamily EXOCOETOIDEA

HEMIRHAMPHIDAE (EVOLANTIIDAE?)

Branchiostegals. Vary from 10–14 with 3 epihyal, 9 ceratohyal, and 1 hypohyal. *Hyporhamphus* 13, *Hemirhamphus* 10–14, *Fodiator* 10–12, *Zenarchopterus* 10–11, *Euleptorhamphus* 10, *Dermogenys* 10. *Hyporhamphus unifasciatus* 13 with 3 epihyal, 9 ceratohyal, and 1 hypohyal, all external except the anteriormost which is free, all laminar acinaciform, curving to about halfway up the gill cover. *Dermogenys sumatranus* 10 with 2 epihyal, 7 ceratohyal, and 1 free, all but the last external. Bases of branchiostegals only slightly expanded. In a sample of 34 *Fodiator acutus* from a single collection the following variation was encountered: 10 (9 specimens), 11 (20), and 12 (5).

Hyoid arch. Interhyal and upper hypohyal absent; epihyal and ceratohyal sutured; hypohyal projects into ventral margin of the ceratohyal.

References. Chevey (1932), Day (1875), Hubbs (1920), Smith, J.L.B. (1955), Weber and de Beaufort (1922).

Material examined. Hyporhamphus unifasciatus, alizarin specimen, NMC62-246, San Lucas, Mexico; *Fodiator acutus*, 34 alcoholic specimens, BC61-116, Acapulco, Mexico.

EXOCOETIDAE (OXYPORHAMPHIDAE)

Pl. 15

Branchiostegals. Vary from 10–13 with 2 epihyal, 7–8 ceratohyal, and 0–3 hypohyal, all being on the external face of the hyoid arch except for the anterior 0–3 which lie free in the gill membrane. *Oxyporhamphus* 10, *Exocoetus* 10–11, *Fodiator* 11, *Cypselurus* 11–13, *Prognichthys* 10–12. *Cypselurus furcatus* 12 with 2 epihyal, 7 ceratohyal, and 3 hypohyal, all on the external face of the arch except the anterior 3 which lie free in the gill membrane, all acinaciform. *Cypselurus californicus* 10 with 2 epihyal and 8 ceratohyal, all acinaciform (anteriormost ray missing?). *Fodiator acutus* 11 with 2 epihyal, 7 ceratohyal, and 2 hypohyal, all on the external face of the arch except for the anterior two which lie free in the gill membrane, all acinaciform and curving halfway up behind the gill cover.

Hyoid arch. Interhyal and upper hypohyal absent; epihyal and ceratohyal joined by interdigitating prongs; hypohyal set into the ventral border of the ceratohyal.

Taxonomy. Parin (1963) includes the Oxyporhamphidae in the Exocoetidae.

References. Abe (1953, 1954*b*), Brunn (1935), Day (1875), Parin (1960), Smitt (1892).

Material examined. Cypselurus californicus, skeletal specimen, USNM 26907, California; *Cypselurus furcatus*, alizarin specimen, BC59-529, Gulf of Mexico, U.S.A.; *Fodiator acutus*, alizarin specimen, NMC58-197, Mexico.

Order PLEURONECTIFORMES

Pl. 14

Branchiostegals 6–7(8) with 2–4 epihyal and 3½–5 ceratohyal, 4 external and 2–3 ventral (sometimes the anteriormost external), all aciniform, the mesial branchiostegal of each side sometimes in contact. Interhyal, epihyal, ceratohyal, and two hypohyals present. Epihyal and ceratohyal sutured together. Ceratohyal sometimes with beryciform foramen. Opercular bones complete, operculum sometimes frayed posteriorly into strands; suboperculum with slender posterodorsal extension. Gill membranes separate or united and free from isthmus. Two suborders, seven families, one of which is known only from fossils. Lower Eocene to recent.

Hubbs (1920) considered the branchiostegals of *Solea* to be of the acanthopterygian type. According to Regan (1929) *Psettodes* is a typical percoid, aside from asymmetry, and might almost be placed in the Serranidae. In comparing flatfishes with *Epinephelus*, *Gadus*, and *Zeus* Norman (1934) found the flatfishes closest to *Epinephelus*.

I agree with designating the pleuronectiform branchiostegals as acanthopterygian. Further, the ceratohyal foramen and frequent presence of 7 branchiostegals would indicate derivation from a primitive perciform or from a beryciform. The low number of caudal rays of primitive Pleuronectiformes would favour derivation from perciform ancestors rather than from beryciform ancestors, but the pelvic count of 5–6 (secondarily to 13) soft rays would suggest a less advanced ancestor.

The torsion of the head in Pleuronectiformes has not notably influenced the branchiostegal series or hyoid arch. This is doubtless because the torsion of the cranium is mainly restricted to the orbital region. The jaws, gills, and branchiostegals are much less affected. The sliding valve is a flap of skin underlying the bases of the gill membranes of certain pleuronectiform families.

The discovery that the anterior branchiostegal contacts its counterpart on the other side in the Soleoidea as well as in the Pleuronectoidea makes the hypothesis of diphyletic origin of the Pleuronectiformes highly unlikely. A somewhat similar character is known only in the Synbranchidae where the anterior branchiostegal of one side crosses its counterpart. This feature probably functions to strengthen the weak and otherwise unsupported centre section of the united gill membrane.

The pleuronectiforms appear closer to the basal than the advanced perciforms and are therefore placed before rather than after the perciforms.

Suborder Psettodoidei

PSETTODIDAE

Branchiostegals. 7 in *Psettodes.*
References. Day (1875), Hubbs (1945*a*), J.L.B. Smith (1950).
Material examined. None.

†JOLEAUDICHTHYIDAE

Branchiostegals. No data available.

Reference. Chabanaud (1937).
Material examined. None.

Suborder **Pleuronectoidei**

Superfamily PLEURONECTOIDEA

BOTHIDAE
Pl. 14

Branchiostegals. Vary from 6–7. *Scophthalmus* (=*Rhombus*) 7, *Pseudorhombus* 6–7, *Bothus* 6–7, *Monolene* 7, *Platophrys* 7, *Lepidorhombus* 7, *Zeugopterus* 7. *Scophthalmus aquosus* 7 with 2 epihyal and 5 ceratohyal, 4 external and 3 ventral, all acinaciform. *Paralichthys lethostigma* 7 with medial one on each side touching the other distally. The medial branchiostegals of each side are separated in *Scophthalmus,* but in the Bothinae and Paralichthyinae the inner branchiostegals of each side meet posteriorly to form a V.
Hyoid arch. In *Scophthalmus* consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal sutured together. Lower hypohyal sends a prong into the ceratohyal. The ceratohyal with a beryciform foramen.
References. Day (1875), Fowler (1936), Garman (1899), Hubbs (1945*a*), Smitt (1892).
Material examined. Scophthalmus aquosus, alizarin specimen, NMC60-207, Magdalen Islands, Quebec; alcoholic specimen, BC55-491, Lower Chesapeake Bay, Virginia; *Paralichthys lethostigma,* alcoholic specimen, BC55-320, Louisiana.

CITHARIDAE

Branchiostegals. 6 in *Lepidoblepheron ophthalmolepis.* The lowest ray of each side not in contact with the other.
References. Hubbs (1945*a,* 1946), Smith (1950).
Material examined. None.

PLEURONECTIDAE
Pl. 14

Branchiostegals. Usually 7(8). *Hippoglossus* 7, *Hippoglossoides* 7 (8), *Limanda* 7, *Reinhardtius* 7, *Pleuronectes* 7, *Lepidopsetta* 7, *Lyopsetta* 7, *Microstomus* 7, *Psettichthys* 7, *Glyptocephalus* 7, *Platichthys* 7, *Psettichthys* 7. *Lepidopsetta bilineata* 7 with 3 epihyal and 4 ceratohyal, 4 external and 3 ventral; *Lyopsetta exilis, Psettichthys melanostictus,* and *Platichthys stellatus* 7 with 2½ epihyal and 4½ ceratohyal, 4 external and 3 ventral; *Microstomus pacificus* and *Hippoglossoides elassodon* 7 with 3½ epihyal and 3½ ceratohyal, 4 external and 3 ventral; *Glyptocephalus zachirus* 7 with 4 on the external epihyal and 3 on the ventral ceratohyal; in all species curved acinaciform; the seventh ray of each side closely approximated at the tip forming a V or a Y.
Hyoid arch. Complete in all examined with interhyal, epihyal, ceratohyal, and two hypohyals; the epihyal and ceratohyal joined by a suture.

TELEOSTEI
MALACOPTERYGII
OR
LOSTEI
ACANTHOPTERYGII
CLUPEIFORMES
NOTACANTHIFORMES
CYPRINIFORMES
MORMYRIFORMES
ANGUILLIFORMES
SACCOPHARYNGIFORMES
GIGANTURIFORMES
MYCTOPHIFORMES
MIRAPINNIFORMES
CTENOTHRISSIFORMES
BERYCIFORMES
ZEIFORMES
LAMPRIDIFORMES
CETOMIMIFORMES
BATHYCLUPEIFORMES
SYNGNATHIFORMES
GADIFORMES
OPHIDIIFORMES
ATELEOPIFORMES
ATHERINIFORMES
PLEURONECTIFORMES
OPHICEPHALIFORMES
PERCIFORMES
ECHENEIFORMES
PERCOPSIFORMES
GASTEROSTEIFORMES
ICOSTEIFORMES
MASTACEMBELIFORMES
SYNBRANCHIFORMES
GOBIESOCIFORMES
BATRACHOIDIFORMES
LOPHIIFORMES
PEGASIFORMES
TETRAODONTIFORMES
8

References. Day (1875), Gregory (1933), Hubbs (1945), Kobayashi and Ueno (1956), Smitt (1892).
Material examined. The following are all alizarin specimens: *Psettichthys melanostictus,* NMC62-215 & S, Vancouver, B.C.; *Lepidopsetta bilineata,* BC56-83, Saturna Island, B.C.; *Lyopsetta exilis,* BC53-40-A, Vancouver, B.C.; *Microstomus pacificus,* BC54-95, Vancouver, B.C.; *Glyptocephalus zachirus,* BC54-95, Vancouver, B.C.; *Hippoglossoides elassodon,* BC54-95, Vancouver, B.C.; *Platichthys stellatus,* uncatalogued, Inst. Fish., University of British Columbia.

Superfamily SOLEOIDEA

SOLEIDAE

Branchiostegals. Vary from 6–7(8). *Achirus* 7, *Solea* 6–7, †*Turabuglossus* 7, †*Eobuglossus* 7, *Paraplagusia* 6, *Soleichthys* 6, *Synaptura* 6. The lowest branchiostegal of each side touches the other on its mesial portion (contrary to Schmidt *in* Norman, 1934).
Hyoid arch. Consists in *Achirus* of interhyal, epihyal, ceratohyal, and at least one hypohyal. Epihyal and ceratohyal sutured together.
References. Chabanaud (1937), Day (1875), Hubbs (1945*a*), Smitt (1892).
Material examined. Achirus mazatlanus, alizarin specimen, NMC62-67-S, Guaymas, Mexico.

CYNOGLOSSIDAE

Branchiostegals. 6 in *Cynoglossus. Cynoglossus robustus* 6, acinaciform; the anteriormost ray of each side connected closely to its opposite (contrary to Schmidt *in* Norman, 1934).
References. Day (1875), Hubbs (1945*a*), Norman (1934).
Material examined. Cynoglossus robustus, alcoholic specimen, BC58-2, Malaya.

Order OPHICEPHALIFORMES (OPHIOCEPHALIFORMES)

(including Anabantoidei and Luciocephaloidei)

Pl. 16

Branchiostegals 5–6 with 0–3 epihyal and 2–5 ceratohyal, 4(6) external and (0)1–2 ventral or internal, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present. Epihyal and ceratohyal sutured together. Ceratohyal without beryciform foramen. Opercular bones complete, with or without spines. Gill membranes separate or united and free from the isthmus. Six families in three suborders. Early Tertiary to present.

The anabantoids have 0–2 epihyal and 4–5 ceratohyal branchiostegals, and the ophicephaloids have 2–3 epihyal and 2–3 ceratohyal.

Regan (1909, 1910) and Jordan (1923) included the Anabantidae, Luciocephalidae, and Ophicephalidae in the Order Labyrinthici. In 1929, Regan considered that the Anabantidae with the Luciocephalidae and the Ophicephalidae belonged in two separate suborders of the Percomorphi. Berg (1947) raised the Ophicephalidae to ordinal level and included each of the other two families in their own suborder amongst the Perciformes. Liem

(1963) supported the latter changes and recognized four anabantoid families, naming two new ones and reviving another. Freihofer (1963) considers that these families are related and show percoid affinities.

The three groups share some unusual characters. The Anabantidae, Luciocephalidae, and Ophicephalidae share an epibranchial organ, a gas gladder extending beyond the main portion of the body cavity posteriorly under the caudal vertebrae, and parasphenoid teeth. In both groups a disrupted lateral line may be found. Further, the three groups share a special adaptation to breeding in poorly oxygenated water. The eggs which float are usually guarded by one or both parents. It seems very improbable that such unusual characters could be found together in a group of families by chance, and thus these unusual characters must be indicative of common origin.

Parasphenoid teeth are unknown in other acanthopterygians (the Tselfatidae are considered to be a malacopterygian).[1] Either parasphenoid teeth in ophicephaliforms are evidence of primitive affinities or they have been developed secondarily. The absence of any other very primitive characters suggests (as Dr. R. M. Bailey and Gosline (footnote) believe, pers. comm.) that the parasphenoid teeth of ophicephaliforms are a secondary development and are not homologous with those of malacopterygians. (Note: I did not find the eight hypurals in Anabantidae reported by Liem, 1963, p. 32.) But the possession of six pelvic rays in the ophicephaloids indicates that they should be placed before the perciforms (unless this is found to be a secondary condition).

Liem's classification of the anabantoid families is followed.

Suborder **Luciocephaloidei**

LUCIOCEPHALIDAE

Branchiostegals. 5 with 0 epihyal and 5 ceratohyal, 4 external and 1 ventral, all acinaciform. Without true median gular.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal sutured.

References. Webber and de Beaufort (1922)[2].

Material examined. Luciocephalus pulcher, alcoholic specimen, BC58-32, Malaya.

Suborder **Anabantoidei**

ANABANTIDAE

Pl. 16

Branchiostegals. 5–6 with ½–2 epihyal and 4–5 ceratohyal, 4 external and 1–2 ventral, all acinaciform. *Anabas testudineus* 6 with 2 epihyal and 4 ceratohyal, 4 external and 2 ventral; *Ctenopoma* 6 with 1 epihyal and 5

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[1] Gosline (1965, Copeia (2): 186–194) points out that the acanthopterygian pristolepids and nandids also have parasphenoid teeth. Their pertinence to the Ophicephaliformes deserves study.

[2] *See* Liem, Karel F. 1967. A morphological study of *Luciocephalus pulcher*, with notes on gular elements in other recent teleosts. J. Morph. 121(2): 103–134, 23 fig.

ceratohyal, 4 external and 2 ventral; *Sandelia* 5 with ½ epihyal and 4½ ceratohyal, 4 external and 1 ventral.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals in all genera. Epihyal and ceratohyal sutured, at least in *Anabas* (Liem shows no sutures in his figure).
References. Chevey (1932), Day (1875), Liem (1963).
Material examined. Anabas testudineus, alizarin specimen, BC59-497, India.

BELONTIIDAE

Branchiostegals. (5)6 with 0–1 epihyal and 4–6 ceratohyal, 4 external and 1–2 ventral, all acinaciform. *Belontia* 6 with 1 epihyal and 5 ceratohyal; *Betta*, *Trichopsis*, *Macropodus*, and *Colisa* 6 with 0 epihyal and 6 ceratohyal; *Sphaerichthys* and *Trichogaster* 0 epihyal and 5 ceratohyal according to Liem, but 1 epihyal and 4 ceratohyal in the *Trichogaster trichopterus* examined by me.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. In *Trichogaster* epihyal and ceratohyal internally sutured and lower hypohyal united to ceratohyal by an internal prong.
References. Day (1875), Liem (1963).
Material examined. Trichogaster trichopterus, alizarin specimen, NMC62-218-S, from Vancouver Public Aquarium.

OSPHRONEMIDAE

Branchiostegals. Osphronemus 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventralateral, all acinaciform.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals.
References. Day (1875), Liem (1963).
Material examined. None.

HELOSTOMATIDAE

Branchiostegals. 6 in *Helostoma* with 1 epihyal and 5 ceratohyal, all external.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals.
Reference. Liem (1963).
Material examined. None.

Suborder **Ophicephaloidei (Ophiocephaloidei)**

The common origin of this suborder with the Anabantoidei has been previously discussed. The ophiocephaloids differ from the anabantoids in that the branchiostegals have moved posteriorly on the hyoid arch, so that there are more on the epihyal. In this character, in the position of the hypohyals and in the strong suturing of the hyoid bones there are resemblances to the Synbranchiformes; but they differ strongly in the form of the opercular bones.
Taxonomy. As shown by Myers and Shapovalov (1931) *Channa* Scopoli 1777 has priority over its subjective synonym *Ophicephalus* Bloch 1794 (the earlier *Channa* Gronow 1763, Zoophyllacium, has been ruled not available because the principles of zoological nomenclature were not applied in that work—Opinion 267; Scopoli's 1777 work, Introd. Hist. Nat., has on the

other hand been placed on the list of accepted works—Opinion 329). (*Ophiocephalus* Hamilton 1882 is an unjustified emendation of *Ophicephalus* Bloch 1794.) Thus *Channa* is the correct generic name for the snakeheads.

The first published family name is apparently Ophicephaloidei Bleeker 1859. It has priority over Channidae. Since most authors are using Ophicephalidae (70% of sample of 21 examples of available literature since 1950), Ophicephalidae is to be maintained according to Article 40 of the rules. The suborder becomes Ophicephaloidei. According to the Berg system of ordinal names the stem of the order is based on the family name, hence Ophicephaliformes.

OPHICEPHALIDAE (OPHIOCEPHALIDAE, CHANNIDAE)

Branchiostegals. 5 in *Channa gachua* with 3 epihyal and 2 ceratohyal, 4 external and 1 internal; 5 in *C. punctata*; 5 in *C. striata* with 2 epihyal and 3 ceratohyal, 4 external and 1 internal. The species examined all had 5, but Hubbs (1920) reported 4 external + 2 ventral in ophicephalid(s) examined, and Munshi (1960) reports 5 or more for *C. striata.*

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. The epihyal and ceratohyal, the ceratohyal and the lower hypohyal, and the ceratohyal and the upper hypohyal are strongly sutured together.

References. Day (1875), Hubbs (1920), Munshi (1960), Weber and de Beaufort (1922).

Material examined. Channa gachua, alizarin preparation, BC58-32, Malaya; *C. striata*, skeleton, USNM 26760, no local.

Order **PERCIFORMES**

(including Mugiliformes [in part],
Polynemiformes, Coryphaeniformes,
Thunniformes, Dactylopteriformes,
Bathyclupeiformes, Gadopseiformes[1])
Pls. 16–20

Branchiostegals (3)4–7(8) with 0–4 epihyal and 2–6 ceratohyal, 4 (very rarely 3) external and 0–4 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals (one in *Mystinichthys* and perhaps in Dactylopteridae). Epihyal and ceratohyal usually sutured together. Ceratohyal in primitive members with beryciform foramen. Opercular bones complete; operculum with 0–3 spines; suboperculum and interoperculum with (rarely 1–2, seldom more) or without spines. Gill membranes separate, joined to the isthmus, or united and free from the isthmus. Includes 24 suborders, one of which is known only from fossils, and 170 families, seven of which are known only from fossils. Upper Cretaceous to present.

The perciforms appear to be derived from the Berycomorphi according to Regan (1913). In this most authors, including myself, are agreed. The form, number, and arrangement of the branchiostegals and the suturing of the epihyal and ceratohyal of this order are typically acanthopterygian. Linking the Perciformes to the Beryciformes are the beryciform foramens found in some primitive Perciformes (e.g., Serranidae). Specializations such as reduced caudal fins do not permit other sub-perciform acanthopterygians to be ancestral to the Perciformes.

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[1] Whitley, G.P. 1959. The freshwater fishes of Australia. Biogeography and ecology in Australia. Monogr. Biol. 8, p. 148.

The Mugiliformes (in part) are included in the Perciformes. Their pelvics appear to be secondarily subabdominal or abdominal. In all other characters including branchiostegals they agree with the Perciformes. The Scleroparei have also been ordinally separated from the Perciformes, but they differ only in that the second infraorbital is united with the preopercular. These differences appear to be neither so important nor so constant as to warrant separation as orders.

Judging from the number of branchiostegals, the gill membranes, and the hyoid arch, the suborders Percoidei, Carangoidei, Scombroidei, and Cottoidei appear to be most primitive.

Because of the relative constancy of the branchiostegal series, almost always 4–7 in this order, descriptions are presented at the subordinal level rather than the family level. Any distinctive patterns within the suborder are noted. Families examined by me are marked by an asterisk. The figure following the family name is the number of branchiostegals. Then, following the diagonal is the number of genera on which the counts are based, e.g., *Embiotocidae (5) 6/2 (=one or more examples of Embiotocidae examined, branchiostegals rarely 5, usually 6; based on one or more species from each of two genera).

Berg (1947) and Bertin and Arambourg (1958) have placed the Bathyclupeidae in the Bathyclupeiformes amongst malacopterygian orders. Patterson (1964) places them amongst the percoid Perciformes. The acanthopterygian nature of the Bathyclupeidae is clearly demonstrated by the following characters: the protrusible upper jaw bordered principally by the premaxillaries; 4 external plus 3 ventral branchiostegals; beryciform ceratohyal foramen; sutured epihyal and ceratohyal; fin spines; thoracic pelvics. The lack of any known subperciform characters or other distinctive characters places it in the Perciformes. Amongst the Perciformes it belongs with the more primitive members as indicated by the possession of a beryciform foramen; 7 branchiostegal rays; a normal hyoid arch with 2 hypohyals; a supramaxillary; a suborbital shelf; gill membranes separate; epihyal and ceratohyal sutured together; and the retention of the basal number of pelvic and caudal rays. It is included in the Percoidei. Examination of a specimen generously provided by the Museum of Comparative Zoology at Harvard showed the ductus pneumaticus to be absent, contrary to authors; blood vessels in this area may have given rise to the error (*see also* Patterson, 1964).

Patterson (1964) argues for the multiple origin of the Perciformes from the Beryciformes. He suggests that the Polymixioidei may have given rise to the Scorpididae and Serranidae and that the Dinopterygoidei may have given rise to the Carangidae, Acanthuroidei, Balistoidei, Chaetodontidae, and Centrarchidae. If so, then these 'perciform' families have all undergone parallel evolution. However, for the moment, they are left in their conventional places.

Suborder Percoidei

Branchiostegals (3,4)5–7(8) with ½–2 epihyal and 4–5 (6) ceratohyal, (3)4 external and (1)2–3(4) ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal usually sutured together. Ceratohyal with or without beryciform foramen (with foramen or traces in the Serranidae, Centrarchidae, Bathyclupeidae, and Branchiostegidae). Opercular bones complete; 0–3 opercular spines (about half of families with opercular spines); spines on suboperculum and interoperculum lacking (or rarely present—Malacanthidae). Gill membranes separate or united, sometimes joined to isthmus. Three divisions including 53 families.

The three divisions (following Matsubara) appear to have some phylogenetic basis, judging by the branchiostegals; Division I has (4)5–7(8) branchiostegals with gill membranes separate or united; Division II has (3)5–6(7) branchiostegals with gill membranes separate, united, or joined to isthmus; and Division III has (3)5–6 branchiostegals and gill membranes united and free, or joined to isthmus. Thus, Division I would appear to be the most primitive, Division III the most advanced, and Division II the one in between. Serranidae is used in the wide sense until it has received an overall review.

The following are the families included. An asterisk marks each family that has been examined by me.

Division I

*Apogonidae (Cheilodipteridae)[1] 6–8/3; *Arripidae 7/1; *Bathyclupeidae 7/1; *Branchiostegidae (Latilidae) 6/3; *Centrarchidae[2] (5)6–7/8; *Cepolidae 6/1; Emmelichthyidae (Inermiidae) 6–7/1; Enoplosidae 7/1; Glaucosomidae 7/1; Grammistidae 6–7/5; Henichthyidae 7/1; *Histiopteridae[3] 7/1; *Kuhliidae (Duleidae), Pl. 16 6/1; *Lobotidae 6/2; *Malacanthidae 6/2; *Mullidae, Pl. 16, (including barbel) 4–5/3; *Nandidae 6/1; *Ostorhinchidae ((H)Oplegnathidae) 6–7/1; Pempheridae 6–7/2[4]; Percichthyidae[5] (Acropomatidae, Maccullochellidae, Maquariidae) 7/5; *Percidae, Pl. 16, 6–8/7; Plesiopidae 5–6/3; Polycentridae 6/1; *Pomatomidae 7/1; *Priacanthidae, Pl. 17, 6/1; *Pristolepidae 6/1; *Pseudochromidae, Pl. 16, 5?6–7/2; Pseudoplesiopidae 6/1; *Scombropsidae 7/1; *Serranidae, Pl. 16 (Ostracoberycidae, Plectroplitidae, Bostockiidae, Epinephelidae, Cephalopholidae, Chromileptidae, Anthiidae, Rainfordiidae) 6–7/36; *Trichodontidae, Pl. 18, 6/1; *Labracoglossidae 7/1.

Division II

Centropomidae 6–7/2; Coracinidae (Dichistiidae) 6/1; Gadopsidae 6/1;

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[1] Tominaga, Yoshiaki. 1964. Notes on the fishes of the genus *Siphamia* (Apogonidae) with a record of *S. versicolor* from the Ryukyu Islands. Japanese J. Ichthyol. 12 (½): 10–17, 3 pls., 5 figs.

[2] The branchiostegals are in agreement with the phylogeny of the family presented by Branson and Moore (1962), primitive genera having 7 rays, advanced genera having 6 or 5.

[3] =Pentacerotidae

[4] Tominaga, Yoshiaki. 1963. A revision of the fishes of the family Pempheridae of Japan. J. Faculty Sci., U. Tokyo, Sect. 4, 10 (1): 269–290, 13 figs.

[5] *See* Gosline, W.A. 1966. The limits of the family Serranidae, with notes on other lower percoids. Proc. Cal. Acad. Sci. 33(6): 91–112, 10 fig.

*Kyphosidae, Pl. 17, (Cyphosidae, Girellidae) 6–7/3; Lactariidae 7/1; *Leiognathidae, Pl. 17, (Gerridae) 5–6/3; Lethrinidae 6/2; *Lutjanidae (Lutianidae) 6–7/6; Maenidae (Centracanthidae) 6/3; *Nemipteridae 5–7/7; Pentapodidae 6/1; *Pomadasyidae (Banjosidae, Haemulidae, Gaterinidae) 6–7/7; *Sciaenidae, Pl. 17, 7(8)/8; Scorpididae 7/1; *Sillaginidae 6/1; *Sparidae, Pl. 17, 5–7/13; *Theraponidae 6/1.

Division III

Aplodactylidae (Haplodactylidae) 5–6/3; *Cheilodactylidae (Chilodactylidae) (3)5–6/6; *Chironemidae 6/1; *Cirrhitidae 6/1; Latridae 6/2.

In fifty specimens of the sciaenid, *Elattarchus archidium*, forty-nine were found with seven branchiostegals and one with eight (BC56-234, Paita, Peru).

One of the most distinctive families of this suborder is the Mullidae. These, unlike any other family in the group, have only 4–5 branchiostegals. Three are normally placed on the external face with 2 epihyal and 1 ceratohyal. There may be a small free one. The anteriormost is situated on the elongated anterior tip of the hyoid arch where it serves as the base of the hyoid barbel. This branchiostegal is short, stout, and twisted basally; distally it is cartilaginous and flexible. Lo Bianco (1907) followed the development of the barbel showing how it moves anteriorly to the adult mental position. Starks (1904) figured the hyoid arch and the branchiostegal barbels of *Mulloides* and demonstrated that *Mulloides* is structurally different from the Polymixiidae; hence the outward similarity must be a product of parallel evolution rather than of common ancestry. Another modification of branchiostegals was found in *Priacanthus serrula* where the branchiostegals were spinulose along their ventral edges; these small spines were lacking in *Priacanthus tayenus*.

References. Abe (1957, 1960, 1960*a*), Bailey (1959), de Beaufort (1940), Berg (1949), Berry (1958), Bertin and Arambourg (1958), Caldwell (1962), Chevey (1932), Day (1875), Dineen and Stokely (1956), Fowler (1936, 1959), Gosline (1960*b*), Green (1941), Gregory (1933), Günther (1859, 1860, 1862, 1887), Herre (1933, 1939), Hubbs (1920), Johnson and Hajny (1957), Jordan and Evermann (1896, 1898), Jordan and Fowler (1902), Katayama (1959, 1960), Kimsey and Fisk (1960), Kuang-yu (1956), Matsubara and Iwai (1958), McPhail (1961), Meek (1904), Meek and Hildebrand (1923, 1925), Okada and Suzuki (1954), Randall (1963), Robins and Starck (1961), Schroeder (1930), Schultz (1958), Smith, J.L.B. (1962), Smitt (1892), Starck and Courtenay (1962), Starks (1904), Weber and de Beaufort (1929, 1931, 1936), Whitley (1959), Woodward (1901), Woolcott (1957).

Suborder Scombroidei

Branchiostegals (5?)6–7(8), usually 7, with 2–3 epihyal and 4–5 ceratohyal, 4 external and 2–3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without beryciform foramen. Opercular bones complete, entire, without spines. Gill membranes separate (except in Luvaridae where joined to isthmus). Ten families, four of which are known only from fossils.

†Blochiidae may not belong here. Romer (1955) placed it questionably in the Heteromi, and Woodward (1942) considered it little different from *Coelorhynchus* and *Pelargorhynchus*.

The following families are included: *Scombridae (Acanthocybiidae, Thunnidae) 7/7; †Palaeorhynchidae 7/1[1]; Istiophoridae (Histiophoridae) 7/1; †Blochiidae—no data available; Xiphiidae 7/1; Gempylidae 7–8/6; †Euzaphlegidae (Zaphlegidae) and †Xiphiorhynchidae—no data available; *Trichiuridae 7–8/6; *Bramidae (Pteraclidae, Steinegeriidae) 7–8/4; Luvaridae 5?–6/1.

The Trichiuridae are peculiar in that the posterior border of their subopercular and opercular bones is fimbriate, the borders being smooth in the other families. The Trichiuridae differ from the Scombridae and Istiophoridae in that the ceratohyal sends a narrow rod under the posterior portion of the lower hypohyal.

References. Abe (1952, 1953*a*, 1961), Bolin (1940), Danilchenko (1960), David (1943), Day (1875), Fowler (1936, 1959), Garman (1899), Günther (1887), James (1961), Jordan (1919), Jordan and Evermann (1896), Khanna (1961), Matsubara and Iwai (1952), Maul (1948, 1954), Mead (1964), Okada and Suzuki (1956), Smitt (1892), Tucker (1956), Weber and de Beaufort (1931), White and Moy-Thomas (1941).

Suborder Carangoidei

Branchiostegals 5–8 with 2–3 epihyal and 3–6 ceratohyal, 4 external and 2–4 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal with beryciform foramen (Carangidae, Formionidae) or without (Rachycentridae). Opercular bones complete, entire, and without spines. Gill membranes usually separate, sometimes united and free from or joined to isthmus. Eight families, one known only from fossils.

The following families are included: †Ioscionidae—no data available; *Carangidae (Nematistiidae), Pl. 17, 7–8/8; *Coryphaenidae 8/1; Leptobramidae 6/1[2]; *Formionidae 7/1; Menidae 7/1; *Rachycentridae 7/1.

The Carangidae is the most primitive family, having more branchiostegals, the gill membranes separate, and a beryciform foramen; Luvaridae are the most advanced, having the fewest branchiostegals and the gill membranes joined to the isthmus.

References. Berry (1959), Day (1875), Fields (1962), Fowler (1936, 1959), Gregory and Conrad (1943), Hubbs (1920), Jordan and Evermann (1896), Meek and Hildebrand (1925), Merriman (1943), Smitt (1892), Weber and de Beaufort (1931), Woodward (1901).

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[1] About ten branchiostegals appear in palaeorhynchids shown in Plate 9 of Obruchev (1964). If this is correct, then the palaeorhynchids (or at least these specimens) are incorrectly placed in the Scombroidei (Obruchev, 1964. Osnovi paleontologii. Bescheliostnie, ribi. Moscow, 522 p.).

[2] Tominaga, Yoshiaki. 1965. The internal morphology and systematic position of *Leptobrama mülleri*, formerly included in the family Pempheridae. Japanese J. Ichthyol. 12 (3/6): 33–56, 10 figs.

Suborder **Kurtoidei**

Branchiostegals 7 with 2 epihyal and 5 ceratohyal, 4 external, 1 internal, and 2 ventral, all acinaciform, the first with an oval base. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured. Ceratohyal with beryciform foramen. Operculars complete, entire. Gill membranes separate.

A single family is included: *Kurtidae 7/1, Pl. 18.

References. de Beaufort and Chapman (1951), Bertin and Arambourg (1958), Boulenger (1904), Day (1875).

Suborder **Mugiloidei**

Branchiostegals (5?)6–7 with 2–3 epihyal and 4 ceratohyal, 4 external and 2–3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without beryciform foramen. Opercular bones complete, without spines or at most with a single weak spine. Gill membranes separate. Two families.

Following Rosen (1964) the Phallostethidae and Atherinidae are removed to the Atheriniformes.

The following families are included: *Sphyraenidae 7/1; *Mugilidae (5)6/4.

References. Berg (1949), Day (1875), Hubbs (1920), Jordan and Evermann (1896), Meek and Hildebrand (1923), Smitt (1892), Weber and de Beaufort (1922), Williams (1959).

Suborder **Polynemoidei**

Branchiostegals 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without beryciform foramen. Opercular bones complete, without spines (operculum and suboperculum fimbriate on posterior borders in *Polydactylus*). Gill membranes separate. A single family.

A single family is included: *Polynemidae 7/2, Pl. 18.

References. Chevey (1932), Day (1875), Hubbs (1920), Jordan and Evermann (1896), Weber and de Beaufort (1922).

Suborder **Trachinoidei**

Branchiostegals 6–7 with 1–2 epihyal and 4–6 ceratohyal, 4 external and 2–3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present (only examined in Bathymasteridae). Epihyal and ceratohyal sutured together (Ophisthognathidae) or not (Bathymasteridae). Ceratohyal without beryciform foramen. Opercular bones complete with 0–2 spines on the operculum, none on the suboperculum, and none or one on the interoperculum. Gill membranes separate, united to each other and free from or joined to the isthmus. Twelve families plus one *incertae cedis* family provisionally placed here.

Regan (1913), in reviewing this group, considered it an unsatisfactory and perhaps artificial assemblage. The characters considered here confirm this opinion. Schultz (1941) united the Kraemeriidae (not followed here) and the Limnichthyidae with the Trichonotidae (followed here). Rofen (1958) considered the Kraemeriidae closest to *Trichonotus* (not followed here). Gosline (1955) removed the Kraemeriidae to the Gobioidei (followed here). *See* Gobioidei.

The following families are included: *Parapercidae (Mugiloididae, Pinguipedidae) 6/2; *Pteropsaridae (Percophidae, Percophididae, Bembropsidae) 5–7/2; Trachinidae 6/1; Creediidae 7/1; *Hemerocoetidae 6–7/1; *Trichonotidae (Limnichthyidae) 6–7/3; *Opistognathidae (Opisthognathidae) 6/1; Owstoniidae 6/1; *Bathymasteridae 6/1; Champsodontidae 6–7/1; Chiasmodontidae 6–7/1; *Cheimarrichthyidae (Chimarrichthyidae) 6/1[1]; Oxudercidae—*incertae sedis*, no data available.

References. de Beaufort and Chapman (1951), Day (1875), Fowler (1936), Ginsburg (1955), Gosline (1963), Gregory (1933), Günther (1861), Hubbs (1920), Meek and Hildebrand (1928), Myers (1935, 1939), Ogilby (1895, 1898), Okada and Suzuki (1952), Okamura and Kishida (1963), Regan (1913), Sato and Ueno (1953), Schultz (1941), Smitt (1892).

Suborder **Uranoscopoidei**

Branchiostegals 6(7) with 1(2) epihyal and (4)5 ceratohyal, 4 external and 2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together or not. Ceratohyal without beryciform foramen. Opercular bones complete, spineless; operculum and suboperculum frayed into rays (except Leptoscopidae). Gill membranes separate or united and free from the isthmus. Three families.

Starks (1923) considered the Uranoscopoidei to be related to the blennioid fishes. The Trichodontidae are similar to the uranoscopoids in having fringed lips and mesopterygoid reduced or absent. The Trichodontidae share lacrimal spines with the Uranoscopidae and dermal hyoid fringes with the Dactyloscopidae. A detailed comparison would be valuable.

The following families are included: *Leptoscopidae 6/1; *Uranoscopidae 6/7; *Dactyloscopidae 6/4.

References. de Beaufort and Chapman (1951), Day (1875), Fowler (1936, 1959), Garman (1899), Gregory (1933), Hubbs (1920), Jordan and Evermann (1898), Miller and Briggs (1962), Myers and Wade (1946), Regan (1913), Starks (1923).

Suborder **Stromatioidei**

Branchiostegals 5–7 with 2 epihyal and 4–5 ceratohyal, 4 external and 2–3 ventral, all acinaciform. Epihyal and ceratohyal sutured together. Beryciform foramens just found in Centrolophidae, Nomeidae, and Ariommidae suggest a more basal position. Opercular bones complete, without spines. Gill membranes separate, united and free from or joined to isthmus. Five families.

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[1] *See* Lane, E. D. 1965. The osteology of *Cheimarrichthys fosteri* Haast. Trans. Roy. Soc. New Zealand, Zool. 6(20): 207–213, 10 figs.

The upper Cretaceous genus *Omosoma* has been previously included in the Stromateidae but is here included in the Polymixiidae (Beryciformes).

The following families are included: Centrolophidae 7/6; Nomeidae 6/2; Ariommidae 6/1; Tetragonuridae 5–6/1; *Stromateidae (Pampidae) 5–6/2.
References. Abe (1953*a*, 1954, 1954*a*, 1955, 1959*a*), de Beaufort and Chapman (1951), Day (1875), Fowler (1936), Grey (1955), Jordan and Evermann (1896), Kobayashi (1961), Ueno (1945*a*). (*See* Note 5, Addenda.)

Suborder Chaetodontoidei

Branchiostegals 4–7 with 1–3 epihyal and 3–5 ceratohyal, 4 external and 0–3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together or separate. Ceratohyal with an apparently non-beryciform foramen (Ephippidae, Toxotidae), or without (Acanthuridae). Opercular bones complete, spineless. Gill membranes united and free from or joined to isthmus. Eight families.

The Zanclidae and Acanthuridae appear to be related to one another and differentiated from the other families by having only 4–5 branchiostegals. The Ephippidae (*Parapsettus*) are peculiar in that their lower two branchiostegals are buried in the muscle of the isthmus and in that their gill opening is restricted.

The following families are included: *Monodactylidae (Psettidae, Amphistiidae) 6–7/1; Toxotidae 7/1; Drepanidae (Drepanichthyidae) 6/1; *Ephippidae (Platacidae, Chaetodipteridae) 6–7/4; *Chaetodontidae (5?)6–7/3; Scatophagidae 6–7/1; *Zanclidae 4/1; *Acanthuridae (Nasidae, Hepatidae), Pl. 19, 4–5/2.
References. Chevey (1932), Day (1875), Fowler (1936, 1959), Gregory (1933), Hubbs (1920), Jordan and Evermann (1898), Meek and Hildebrand (1928), Weber and de Beaufort (1936).

Suborder Embiotocoidei

Branchiostegals (5)6 with 2–2½ epihyal and 3½–4 ceratohyal, 4 external and 2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without beryciform foramen. Opercular bones complete, spineless. Gill membranes united and free from isthmus or slightly joined to it. A single family.
One family is included: *Embiotocidae (5)6/2, Pl. 18.
References. Hubbs (1920), Jordan and Evermann (1898), Tarp (1952).

Suborder Pomacentroidei

Branchiostegals (4)5–6 with 1–3 epihyal and 3–4 ceratohyal, 4 external and 1–2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without beryciform foramen. Operculars complete, spineless. Gill membranes united and free from isthmus. Two families.

The following families are included: *Cichlidae 5–6/3; *Pomacentridae (4)5–6/10.

References. Chevey (1932), Fowler (1959), Hubbs (1920), Jordan and Evermann (1898), Kamohara (1960), Meek (1904), Meek and Hildebrand (1925), Travassos and Pinto (1959).

Suborder Notothenioidei

Branchiostegals 5–7 with 2 epihyal and 4–5 ceratohyal, 4 external and 2–3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal not sutured together (Nototheniidae). Ceratohyal without beryciform foramen (only Nototheniidae examined). Opercular bones complete; operculum with 0–3 spines; suboperculum and interoperculum with 1 spine (Chaenichthyidae) or none. Gill membranes separate (Bovichtidae) or united and free from the isthmus or joined to the isthmus (other families). Five families.

The following families are included: *Bovichtidae (Bovichthyidae) 7/1; *Nototheniidae, Pl. 18, (5)6–7/3; Harpagiferidae 5/1; Bathydraconidae[1] 7/3; Channichthyidae (Chaenichthyidae) 6/1.

References. de Witt and Tyler (1960), Dollo (1904), Gregory (1933), Regan (1913*a*).

Suborder Ammodytoidei

Branchiostegals (6)7(8) with 2 epihyal and 5 ceratohyal, 4 external and 3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal separate. Ceratohyal without beryciform foramen. Opercular bones complete, spineless; posterior ventral border of suboperculum dissected into rays. Gill membranes separate.

Two families are included: *Ammodytidae (Bleekeridae), Pl. 19, (6)7(8)/2; Hypoptychidae 4/1.

References. Beebe and Tee-Van (1938), Fowler (1936), Gosline (1963), Hubbs (1920), Jordan and Evermann (1896), Smitt (1895).

Suborder Callionymoidei

Branchiostegals 5–7 with 3–4 epihyal and 2–3 ceratohyal, 4 external and 2 ventral, all acinaciform or filiform. Interhyal, epihyal, ceratohyal, and two hypohyals present. Ceratohyal without beryciform foramen. Opercular bones complete and entire (Callionymidae) or operculum and suboperculum with spine (Draconettidae). Gill membranes joined to isthmus. Two families.

In the Callionymidae the gill opening is restricted to a small foramen on the upper side of the head, and the branchiostegals become filiform terminally. In the Draconettidae the gill opening is broader, extending to just above the pelvic base, and the branchiostegals are acinaciform. It would appear that in the Callionymidae the branchiostegals no longer possess the function of moving the gill membrane (which became broadly connected to the isthmus and lower side of the body) and have retained only the function of support. With only a supporting function the branchiostegals degenerated from an acinaciform to a filiform condition, much as they have in the eels.

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[1] Counts of 6 and 10 are in error for *Bathydraco* (de Witt and Tyler, 1960).

Two families are included: *Callionymidae 5–7/1; *Draconettidae 6/1. *References.* Briggs and Berry (1959), Day (1875), Fowler (1936), Garman (1899), Gregory (1933), Jordan and Evermann (1898), Smitt (1892).

Suborder **Blennioidei**

Branchiostegals 4–7(8) with 1–2 epihyal and 3–5 ceratohyal, 4 external and 1–3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together or not. Ceratohyal without beryciform foramen. Opercular bones complete, spineless (except that the Congrogadidae may have an opercular spine). Gill membranes united and free from the isthmus or joined to the isthmus. Seventeen families, one of which is known only from fossils.

The following families are included: *Tripterygiidae 6–7/1; †Pterygocephalidae 5/1; Chaenopsidae 6/10; Clinidae (Ophiclinidae, Ophioclinidae) (5)6(7)/11; Blenniidae (5)6(7)/9; *Congrogadidae (Haliophidae) 4 or 6/5; Peronedyidae 4/1; *Zoarcidae (Lycodapidae, Derepodichthyidae), Pl. 19, (4)5–6(7)/14; *Scytalinidae 6/1; *Anarhichadidae 6–7/3; *Stichaeidae (Lumpenidae, Xiphisteriidae, Cebedichthyidae) 6/2; *Zaproridae 6/1[1]; Pholididae 5–6(7)/2; *Ptilichthyidae 6/1; *Cryptacanthodidae 6/1; Xenocephalidae—no data available; Notograptidae—no data available.

Makushok (1958) gives a count of 3 branchiostegals for *Ptilichthys*, and Bean (1882) gives 5. Kobayashi (1961) and I have found 6 branchiostegals (4 specimens examined).

References. Andriashev (1955), Barsukuv (1959), de Beaufort and Chapman (1951), Beebe and Tee-Van (1938), Berg (1949), Böhlke (1961), Borodin (1933), Chapman and Townsend (1938), Clemens and Wilby (1961), Day (1875), Fowler (1936, 1959), Garman (1899), Gosline (1963), Gregory (1933), Günther (1867), Hubbs (1920), Hubbs, Clark (1952, 1953), Jordan and Evermann (1898), Kobayashi (1961*a*), Makushok (1958, 1961, 1961*a*), McAllister and Krejsa (1961), Norman (MS.), Ogilby (1898), Regan (1912), Smith, C.L. (1957), Smith, J.L.B. (1952, 1961), Smitt (1892), Stephens (1961), Ueno (1954).

Suborder **Schindlerioidei**

Branchiostegals 5 with 2 epihyal and 3 ceratohyal, 3 external and 2 ventral, all acinaciform. Interhyal, epihyal, and ceratohyal present; hypohyals not present. Interhyal (cartilaginous) articulates with the head instead of the base of the hyomandibular; epihyal and ceratohyal ossified and sutured dorsally; ceratohyal without beryciform foramen. Operculum present, slender, spineless; interoperculum and suboperculum absent. A single family.

Gosline (1959) indicates that this family is unique in its caudal skeleton and the insertion of the hyoid arch. But a somewhat similar condition is also found in the tiny goby, *Mystichthys luzonensis*. There is a cartilaginous interhyal present in the specimens studied, unlike Gosline's, and the epihyal and the ceratohyal are joined dorsally by a suture. The interhyal inserts on the head of the hyomandibular instead of in the normal position on the lower end of the hyomandibular. However, in developing embryos, such as *Gasterosteus* (*see* de Beer, 1937, pl. 57, 4.2-mm stage), the interhyal inserts just below the head of the hyomandibular; by the 25-mm stage the interhyal has moved down towards the lower tip of the hyomandibular in the normal adult position, with the tip of the hyomandibular forming the symplectic. Thus, the condition of the hyoid arch in Schindleriidae is probably not a new development but representative of the retention of the larval condition, a retention not unexpected in a neotenic fish. This retention agrees with Gosline's general statement that the "ossifications" that do occur in Schindleriidae are not of the adult fish type at all but are merely calcifications of normally larval structures. A further modification from the normal acanthopterygian condition is the possession of only 5 branchiostegal rays, the uppermost (external) ray having been lost. Normally in fishes only the ventral branchiostegals are lost leaving 4 branchiostegals on the external face of the hyoid, instead of only the 3 found in Schindleriidae.

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[1] Ueno and Abe (1964, Bull. Hokkaido Regional. Fish. Res. Lab. (28): 1–22, 14 figs.) report 5 in two specimens off Kushiro; Chapman and Townsend (1938) and McAllister and Krejsa (1961) found 6 in skeletons or cleared and stained specimens.

A single family is included: *Schindleriidae 5/1.

References. de Beaufort and Chapman (1951), Giltay (1934), Gosline (1959).

Material examined. Schindleria praematura, 2 alizarin specimens, Inst. Fish., University of British Columbia, Islas Revillagigedo at southeast end of Isla Clarion, Mexico, identified by Dr. R. Rosenblatt.

Suborder **Labroidei**

Branchiostegals 5–6 with 1 epihyal and 4 ceratohyal, 4 external and 1 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together or not. Ceratohyal without beryciform foramen. Opercular bones complete, spineless. Gill membranes united and free from or joined to the isthmus. Three families.

The following families are included: *Labridae (Coridae, Bodianidae) 5–6/15; *Scaridae (Calliodontidae) 5/4; *Odacidae 5/1.

References. de Beaufort (1940), Chevey (1932), Day (1875), Fowler (1936, 1959), Hubbs (1920), Jordan and Evermann (1898), Meek and Hildebrand (1928), Schultz (1958), Smitt (1892).

Suborder **Gobioidei**

Branchiostegals (3) 4–7 with 1–2 epihyal and 4–5½ ceratohyal, 4 external and 2–3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present (except only one ossified hypohyal in *Mystinichthys*); epihyal and ceratohyal separate. Ceratohyal without beryciform foramen. Opercular bones complete and spineless (may have soft points). Gill membranes joined to the isthmus. Eight families, one known only from fossils.

The Kraemeriidae have often been placed near the Trichonotidae. Gosline (1955), however, moved them to the Gobioidei (along with the Microdesmidae). Rofen (1958) was lead to believe that the genus *Trichonotus* is the closest relative of the Kraemeriidae. The present study favours Gosline's view. The branchiostegals number 5 in the Kraemeriidae with 1 on the epihyal; the gill membranes are joined to the isthmus. In all the Trachinoidei examined the branchiostegals are 6–7 with 2 on the epihyal, and the gill membranes are seldom joined to the isthmus. On the other hand, the branchiostegals in the Gobioidei are usually 5 (3–6) with 1–2 on the epihyal, and the gill membranes are always joined to the isthmus. This is then evidence for placement of the Kraemeriidae in the Gobioidei. In the tiny goby (up to 14 mm), *Mystichthys luzonensis*, the interhyal inserts above the ventral end of the hyomandibular, as in the neotenic Schindleriidae, and only the lower hypohyal is ossified.

Some eleotrids are distinctive in having branchiostegal spines. *Belobranchus* has a sharp spine directed upwards and forwards on the first or first and second branchiostegals, whereas *Valenciennea, Pteroculiops*, and *Diaphoroculius* usually lack spines but occasionally have one. The Trypaucheninae (Taenioididae) are peculiar in having a separate opening at the top of the operculum leading to a cavity separate from the gill cavity.

See under Ophidiiformes discussion of possible relationships of the Gobioidei.

Gosline (1955) indicated that the distribution of the branchiostegals is peculiar in the Gobioidei, although this does not appear to be distinctive to me. However, the gobioids are distinct from many perciforms in that the uppermost branchiostegal is notably broader than the remainder of the series, being somewhat sickle-shaped.

The following families are included: †Pirskeniidae, 6–7/1; * Eleotridae, Pl. 19, 4–6/6; Milyeringidae 7/1; *Gobiidae (Periophthalmidae), Pl. 19, 3–5/16; Rhyacichthyidae 6/1; Taenioididae 5/1; Kraemeriidae 5/1; Microdesmidae (Cerdalidae, Pholidichthyidae, Gunnelichthyidae) (4)5–6/1.

References. Böhlke and Robins (1960, 1960*a*, 1961), Day (1875), Fowler (1936), Garman (1899), Gosline (1955), Günther (1861), Herre (1945), Hubbs (1920), Jordan and Evermann (1898), Koumans (1953), Matsubara and Iwai (1959), Myers and Wade (1946), Norman (MS.), Obrhelová (1961), Rofen (1958), Te Winkel (1935), Whitley (1945).

Suborder **Siganoidei**

Branchiostegals 5 with 1½ epihyal and 3½ ceratohyal, 4 external and 1 ventral, all acinaciform. The lowest branchiostegal broad and buried in the isthmus (as in Ephippidae). Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without beryciform foramen. Opercular bones complete, spineless. Gill membranes joined to isthmus.

A single family is included: *Siganidae 5/1.

References. Chevey (1932), Day (1875), Hubbs (1920), Jordan and Fowler (1902*a*).

†Suborder **Rhamphosoidei**

No data available on branchiostegals, operculars, or hyoid arch. Rhamphosoidei has been placed with the hemibranchs (Eastman, 1914), in the Ammodytoidei (Romer, 1955), and its own suborder of the Perciformes (Berg, 1955).[1]

A single family is included: Rhamphosidae (Ramphosidae)—no data/1.

Suborder **Cottoidei**

Branchiostegals (4)5–7(8) with 1–2 epihyal and 4–6 ceratohyal, 4 external and 1–3(4) ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals; epihyal and ceratohyal sutured together or not. Ceratohyal without beryciform foramen. Opercular bones complete; 0–3 spines on operculum and 0–1, usually 0, on the operculum and suboperculum. Gill membranes separate, united and free from or joined to the isthmus. Twenty-two families.

The following families are included: *Scorpaenidae 6–7(8)/34; Synancejidae (6)7/4; Congiopodidae 5/1; Pataecidae 6/1; Gnathanacanthidae—no data; Aploactidae 5–6/1; Caracanthidae 4–5/1; *Anoplopomatidae 6/1; *Hexagrammidae (Zaniolepidae), Pl. 20, 6–7/1; Parabembridae—no data; Bembridae (Bembradidae) 7/1; *Platycephalidae 7/3; Hophlichthyidae—no data; *Cottidae (Rhamphocottidae), Pl. 20, (5)6–7/14; (in subfamilies *Abyssocottinae and *Cottocomephorinae 6); *Comephoridae 6–7 (family); Normanichthyidae 5/1; *Psychrolutidae 7/1; *Cottunculidae 7/1; *Agonidae, Pl. 20, 6/2; *Triglidae, Pl. 20, 6–7/5; *Peristediidae 7/1.

References. Bolin (1952), Clark (1937), Day (1875), Fowler (1936, 1959), Freeman (1951), Garman (1899), Gill (1891*d*), Gregory (1933), Günther (1860), Hubbs (1920), Jordan and Evermann (1898), MacLeay (1881), Matsubara (1943), Matsubara and Hiyama (1932), Ruttenberg (1954), Schmidt (1928, 1950), Smith, J.L.B. (1950), Smitt (1892), Taranets (1941), Waite (1923), Watanabe (1960), Welander and Alverson (1954), Woodward (1901).

Suborder **Cyclopteroidei**

Branchiostegals 6 with 2 epihyal and 4 ceratohyal, 4 lateral and 2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal separate. Ceratohyal without (true?) beryciform foramen. Operculars complete, spineless. Gill opening restricted. Three families.

The following families are included: *Cyclopteridae 6/1; *Liparidae, Pl. 19, 6/3; Eutelichthyidae 6/1.

References. Burke (1930), Cohen (1960), Fowler (1936), Garman (1899), Hubbs (1920), Smitt (1892, 1895), Tortonese (1959).

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[1] Eigil Nielsen adds to knowledge of its anatomy. The denticulate ornate rostrum recalls that of the Pegasidae (1960. A new Eocene teleost from Denmark. Medd. Dansk. Geol. Foren. 14: 247–252, 3 figs.).

Suborder **Dactylopteroidei**

Branchiostegals 6 with 3 epihyal and 3 ceratohyal, 4 external and 2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and only one hypohyal present (last feature should be checked); epihyal and ceratohyal separate. Ceratohyal without beryciform foramen. Opercular bones complete, small, and spineless. Gill openings reduced. A single family.

This family differs from the Scleroparei in having as many as three branchiostegals on the epihyal, in the reduction in size of its opercular bones, and in having only a single hypohyal. The branchiostegals and related bones thus confirm its placement in a separate suborder.

A single family is included: *Dactylopteridae 6/1.

References. Day (1875), Gill (1891*c*), Hubbs (1920).

Order **GASTEROSTEIFORMES**

Pl. 20

Branchiostegals 3–4 with 1 epihyal and 2–3 ceratohyal, all external, slender, and acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present. Interhyal small. Epihyal and ceratohyal joined by a dorsal suture which forms a strut. Ceratohyal without beryciform foramen. Opercular bones complete, entire, without spines. Gill membranes joined to isthmus or united and free from the isthmus. Eocene to present. Three families, one wholly fossil; and one family provisionally included here.

The relationships of this group and the reasons for separation of it from the Syngnathiformes are discussed under the Syngnathiformes.

The Upper Cretaceous †*Protriacanthus* has been indicated (Patterson, 1964) as belonging in the Gasterosteiformes or in the Aulostomiformes. Its morphology suggests to me that it belongs to the Gasterosteiformes. Like them it has three branchiostegals (d'Erasmo, 1946).

AULORHYNCHIDAE

Branchiostegals. 4 branchiostegals in *Aulorhynchus flavidum* with 1 epihyal and 3 ceratohyal, all on the external face of the arch, all acinaciform; aside from a basal bend the rays are quite straight.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Interhyal larger at lower end. Epihyal and ceratohyal joined by a suture which forms a stay on the mesial side of the arch. Ceratohyal elongate and swelling a little posteriorly, unlike that of the Gasterosteidae. Lower hypohyal anteriormost, sending a prong backward on the mesial face of the ceratohyal. Upper hypohyal above anterior end of the ceratohyal.

References. Bertin and Arambourg (1958), Jordan and Evermann (1896).

Material examined. Aulorhynchus flavidum, alizarin specimen, NMC61-163-S, San Juan Bautista Island, southeast Alaska; alizarin specimen, BC60-548, British Columbia.

GASTEROSTEIDAE

Pl. 20

Branchiostegals. 3 in *Gasterosteus, Spinachia, Culaea* (=*Eucalia*), *Apeltes,* and *Pungitius*. *Gasterosteus aculeatus* (freshwater type and marine type) 3 with 1 epihyal and 2 ceratohyal, all external, slender acinaciform, and slightly bowed. *Pungitius pungitius* 3 with 1 epihyal and 2 ceratohyal, all external, slender acinaciform, and slightly bowed.

Hyoid arch. In *Gasterosteus, Culaea,* and *Pungitius* consists of interhyal, epihyal, ceratohyal, and two hypohyals; interhyal ends equal, or lower end larger; epihyal and ceratohyal joined by a strut; posterior end of ceratohyal about twice width of anterior end; upper hypohyal lies above anterior end of ceratohyal; lower hypohyal anteriormost sending a prong backward along the lower side of the ceratohyal.

References. Berg (1949), Bertin and Arambourg (1958), Jordan and Evermann (1896), Smitt (1895).

Material examined. Gasterosteus aculeatus (freshwater type), alizarin specimen, Inst. Fish., University of British Columbia; *Gasterosteus aculeatus* (marine type), alizarin specimen, NMC59-441, Ungava Bay, Quebec; *Pungitius pungitius*, alizarin specimen, NMC61-228 & S, McConnell River, Northwest Territories; *Culaea inconstans*, alizarin specimen, NMC61-200, southern Saskatchewan.

†PROTOSYNGNATHIDAE

Branchiostegals. No data available.

Relationships. Woodward (1901) synonymizes *Protosyngnathus* with *Aulorhynchus*. Berg (1947) places it in its own family. The operculum, as figured by Günther, looks more like that of *Aulorhynchus* than that of the syngnathiforms.

References. Berg (1947), Günther (1876), Von der Mark (1876), Woodward (1901).

INDOSTOMIDAE, *incertae sedis*

Branchiostegals. 5–6.

Relationships. Until the osteology of this family is better known its placement is uncertain. The number of branchiostegals and pelvic rays is higher than in Gasterosteidae and Aulorhynchidae. According to Bolin (1936), the majority of characters—body form, fins, teeth, lateral line system, anterior vertebrae, and branchiostegals—link Indostomidae most closely to the Aulorhynchidae and Aulostomidae. The numerous pectoral rays agree more with the Syngnathiformes. The serrated radiating ridges on the operculum are unusual. The branched rays of the median fins agree with the Gasterosteiformes.

References. Berg (1947), Bolin (1936), Prashad and Mukerji (1929).

Material examined. None.

Order ICOSTEIFORMES

Branchiostegals 6–7 with 1–2 epihyal and 4–5 ceratohyal, 4 external and 2 ventral, all acinaciform. Operculars complete, striated with crenulated edges, without spines. Gill membranes separate. Interhyal, epihyal, ceratohyal, and two hypohyals; epihyal and ceratohyal separate; articulating faces of epihyal, ceratohyal, and hypohyals cartilaginous. Ceratohyal without beryciform foramen. Gill membranes narrowly joined to isthmus, nearly separate. A single recent family.

According to Regan (1923*a*) there is nothing in their organization to prevent the assumption that Icosteiformes are specialized and degenerate perciforms. I agree with this opinion; the branchiostegal form and distribution, the spiny scales, the premaxillary bordered upper jaw, the five pelvic rays, and the physoclistic gas bladder all favour derivation from an advanced acanthopterygian order. Such differences as lack of fin spines, non-protractible premaxillaries, and abdominal pelvics may be regarded as secondary modifications.

ICOSTEIDAE

Branchiostegals. Icosteus aenigmaticus 6–7 with 2 epihyal and 4 ceratohyal, 4 on external and 2 on ventral face of hyoid arch. In three specimens examined by me and one reported by Abe (1954*a*) the branchiostegals have numbered 6, but Kobayashi and Ueno (1956) report 7, and Regan (1923) and Jordan and Evermann (1896) report 6–7.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal separated by their cartilaginous unsutured ends.

References. Abe (1954), Jordan and Evermann (1896), Kobayashi and Ueno (1956), Regan (1923*a*).

Material examined. Icosteus aenigmaticus, alcoholic specimen, BC53-99-A, Vancouver Island, B.C.; alcoholic specimen, BC63-09, Hetta Inlet, near Cordova, Alaska; alcoholic specimen, USNM 49163, San Diego, California; alcoholic specimen, BC59-523, off Queen Charlotte Islands, B.C.

Order ECHENEIFORMES

Pl. 20

Branchiostegals 8–11 with 2 epihyal and 6–9 ceratohyal, 4 external and 4–7 on the internal face of the hyoid arch, acinaciform; opercular bones complete and entire (or opercular crenulate), without spines; suboperculum V-shaped, ascending behind and before operculum; gill membranes separate; interhyal, epihyal, ceratohyal, and two hypohyals present, the lower hypohyal invading the lower edge of the ceratohyal; epihyal and ceratohyal sutured. Ceratohyal without beryciform foramen. Eocene or Oligocene to present. Two families, one wholly fossil, the other living.

According to Gill (1883) the Echeneididae approach the Gobioidea and Blennioidea but definitely are not related to the Scombridae and Carangidae which have the basis cranii double. Regan (1912*d*) concluded that they were basically percoid, that their fins were very similar to those of Pomatomidae, Carangidae, and Rachycentridae, and that the Echeneididae may have evolved from percoids of this type. Starks (1930) considered the shoulder girdle of Echeneididae to be considerably like some of the fishes of the family Scombridae, with the cleithrum turned back at the top and extending but little above the scapula. Gregory (1933) suggested that they were derived from relatively primitive percoids such as the stromatioid *Palinurichthys*, the barrelfish, which lurks under logs.

The high number of branchiostegals (8–11) would seem to be best regarded as a secondary multiplication from the usual perciform number of 6 to 8, in the absence of other primitive acanthopterygian characters and in the presence of the standard perciform number of 15 ventral and 15 branched caudal rays. (In their secondary multiplication, but not arrangement, the branchiostegals agree with the beloniforms.) Derivation would seem feasible from one of the primitive perciform suborders. However, there are certain resemblances to some of the subperciforms that would bear investigation.

†OPISTHOMYZONIDAE

Branchiostegals. Not visible in specimen of *Opisthomyzon.*
References. Gudger (1926), Wettstein (1886).
Material examined. None.

ECHENEIDIDAE (ECHENEIDAE)

Pl. 20

Branchiostegals. Vary from 8–11 with 2 epihyal and 6–9 ceratohyal, 4 external and 4–7 on internal face, all acinaciform, curving up behind the suboperculum. *Remoropsis brachyptera* with 9, 2 epihyal and 7 ceratohyal, 4 external and 5 internal; two others also with 9. *Rhombochirus osteochir* 8 (3 specimens) with 2 epihyal and 6 ceratohyal, 4 external and 4 internal; *Remilegia australis* (9) 10–11 with 2 epihyal and 9 ceratohyal, 4 external and 7 internal; *Echeneis naucrates* 9; *Remora remora* 9 (3 specimens) with 2 epihyal and 7 ceratohyal, 4 external and 5 internal. Day (1875), apparently followed by Fowler (1936), reports 7 branchiostegals in *Echeneis, Remora, Remoropsis,* and *Remorina.* Day apparently failed to observe the smaller anterior branchiostegals in the thick skin; consequently his counts are not recorded with the above counts made either by dissection, by alizarin staining of specimens, or by careful external examination. Hubbs (1920) also implied that there were but 6 or 7 branchiostegals in *Echeneis.* Although it is quite possible or even probable that counts of 7 will be found when large series are examined, from the present study it seems that such a count will not be usual.
Hyoid arch. Small interhyal, epihyal, ceratohyal, and two hypohyals present. The epihyal and ceratohyal are joined by interdigitating prongs. The lower hypohyal sends a two-pronged fork into the lower ceratohyal; the upper interhyal lies dorsolaterally to the anterior end of the ceratohyal.
References. Day (1875), Follett and Dempster (1960), Fowler (1936), Hubbs (1920), Jordan and Evermann (1898), Strasburg (1957).
Material examined. Remoropsis brachyptera, alizarin specimen and one alcoholic specimen, BC54-72, San Lucas, Baja California, Mexico; two alcoholic specimens, BC56-435, Galápagos; *Rhombochirus osteochir,* dissected specimen, BC57-171, Las Tres Marias Islands, Mexico; alcoholic specimen, BC59-266, Maria Magdalena Island, Mexico; *Remilegia australis,* alcoholic specimen, BC53-236, Goose Island Banks, B.C.; *Echeneis naucrates,* alcoholic specimen, BC53-180, Columbia; *Remora remora,* skeletal specimen, USNM 265667, 39° N, 72° W: two uncatalogued NMC specimens, from offing of southern Nova Scotia.

Order TETRAODONTIFORMES (TETRODONTIFORMES)

Branchiostegals (3) 5–6 with 0–2 epihyal and 3½–6 ceratohyal, (3) 4 external and 1–2 ventral, lowest branchiostegal (except in Ostraciidae and Molidae) expanded, the rest acinaciform (except Molidae where they secondarily somewhat resemble the spathiform). Interhyal, epihyal, ceratohyal, and two hypohyals present. Epihyal and ceratohyal sutured (except Molidae). Ceratohyal without beryciform foramen. Opercular bones complete, entire, lacking spines (except *Chilomycterus*). Gill openings restricted to sides of head. Four suborders with 11 families; 3 of the families are known only from fossils. Upper Cretaceous to recent.

Regan (1902) believed that there could be no question as to the close relationship of the less specialized forms of Plectognathi (= Tetraodontiformes) to the Acanthuridae, but he considered that the Tetraodontiformes differed ordinally from that family. Hubbs (1920) correctly indicated that the branchiostegals of this group are of the acanthopterygian type. Gregory included the zanclids and teuthids (= acanthurids) in the order. Le Danois (1955), followed by Bertin and Arambourg (1958), removed the Canthigasteridae, Molidae, Tetraodontidae, Diodontidae, and Ostraciidae from the order and placed them amongst the malacopterygians in the group Orbiculati. This change was made on the basis of the lack of spines in the fins (Tyler, 1962, pertinently points out that *Triodon* has spines) and a number of other characters such as feeble ossification of the skeleton (hardly true), medioparietal cranium (not restricted to Malacopterygii), and dorsal and anal opposed to one another on posterior portion of the body (found in acanthopterygians such as Lophiiformes, Pegasiiformes, Echeneiformes, and so on). None of these necessitate placement in the Malacopterygii. Most authors, e.g., Regan, Berg, Gregory, Hubbs, have considered the Tetraodontiformes as acanthopterygian. Tyler (1963) succinctly scuttles Le Danois' classification.

The branchiostegal system is in agreement with Tyler's opinion. The number, form, and arrangement of the branchiostegals and the epihyal-ceratohyal suture are definitely acanthopterygian. The curiously expanded lower branchiostegal is found in members of both of the groups into which Le Danois divides the Tetraodontiformes, indicating the artificiality of the division.

The branchiostegals undergo some interesting variations in this group. In the Ostraciidae there is a tendency towards expansion of the ends of the branchiostegals. In the Molidae the branchiostegals are expanded even more and resemble spathiform branchiostegals except that they are thick and nonlaminar. In the other families, the lowest branchiostegal is expanded distally into an elongate triangle or fan. These expansions may be related to the small gill opening and to the stiffening of the wall of the branchial chamber by thick skin or bony plates. These two factors would probably necessitate a stronger branchial pumping mechanism than is usual. From this strong branchial pumping mechanism may have developed the peculiar inflating habit of some Tetraodontiformes. The puffing Tetraodontiformes belong to the suborders that have the lowest branchiostegal expanded. In the puffing families this branchiostegal is further expanded and strengthened and the upper edge is curled outwards. Tyler (1962) has neatly explained the function of this expanded branchiostegal by ascribing to it the function of the pump which inflates the distensible gut of the puffers.

For †*Protriacanthus*, *see* Gasterosteiformes.

Suborder **Balistoidei**

†EOTRIGONODONTIDAE

Branchiostegals. No data available.
Reference. Woodward (1901).

†SPINACANTHIDAE

Branchiostegals. No data available.
Reference. Woodward (1901).

†TRIGONODONTIDAE

Branchiostegals. No data available; known only from the front teeth.
References. Bauza (1948), Woodward (1901).

TRIACANTHIDAE (TRIACANTHODIDAE)

Branchiostegals. 6 in *Triacanthus oxycephalus* with 2 epihyal and 4 ceratohyal, 4 external and 2 ventral, the upper 3 acinaciform, the next two scimitar-like, the lowest very broad mesially with its greatest width equalling one-third its length.
Hyoid arch. Epihyal and ceratohyal very short and deep.
References. Day (1875), Fraser-Brunner (1941), Gregory (1933).
Material examined. *Triacanthus oxycephalus*, alcoholic specimen, BC59-574, Thailand.

MONACANTHIDAE (ALUTERIDAE)

Branchiostegals. Vary from (3) 5–6. *Stephanolepis* 6, *Alutera* 6, *Osbeckia* 6, *Monacanthus* 5, *Psilocephalus* 3. *Monacanthus hispidus* 5 with 1½ epihyal and 3½ ceratohyal, 4 external and 1 ventral; the lowest broad, laminar, and scimitar-like; the rest acinaciform.
Hyoid arch. In *Monacanthus* consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal sutured together. Ventral hypohyal the anteriormost, the dorsal hypohyal partially over the anterior end of the ceratohyal.
References. Day (1875), Fraser-Brunner (1940), Gregory (1933).
Material examined. *Monacanthus hispidus*, alizarin specimen, BC59-529, Gulf of Mexico.

BALISTIDAE

Branchiostegals. 6 in *Balistes, Xanthichthys*, and *Abalistes*. *Balistes verres* 6 with 4 external epihyal and 2 ventral ceratohyal, the four upper close together. The lowest are laminar and highly curved, and the upper ones are acinaciform.

Hyoid arch. In *Balistes* consists of interhyal, epihyal, ceratohyal, and two hypohyals; epihyal and ceratohyal sutured together, the upper hypohyal more posterior. Ceratohyal normally expanded posteriorly.
References. Day (1875), Fraser-Brunner (1935), Gregory (1933).
Material examined. Balistes verres, alcoholic specimen, BC60-467, Guerrero, Mexico.

Suborder **Tetraodontoidei (Tetrodontoidei)**

TRIODONTIDAE

Branchiostegals. 6 in *Triodon bursarius*, the upper 4 close together on the external face, the lower 2 on the ventral face of the hyoid arch, all acinaciform but the lowest, which is scimitar-shaped and laminar except that the dorsal edge curves out somewhat (not so much as in the tetraodontids and diodontids, according to Tyler, 1962).
References. Day (1875), Tyler (1962).
Material examined. None.

TETRAODONTIDAE (TETRODONTIDAE, CANTHIGASTERIDAE, COLOMESIDAE, LAGOCEPHALIDAE, CHONERHINIDAE).

Branchiostegals. Vary from 5–6. *Canthigaster* 5–6, *Sphaeroides* 5, *Tetraodon* 5–6. *Canthigaster punctatissima* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform except the lowest which is stout and is expanded into a fan, curling outward on the upper edge.
Hyoid arch. In *Canthigaster* at least epihyal, ceratohyal, and one hypohyal present; epihyal and ceratohyal strongly sutured together; ceratohyal with a large triangular ventral projection just anterior to the middle of its length.
References. Day (1875), Fowler (1936), Fraser-Brunner (1943), Hubbs (1920), Tyler (1962).
Material examined. Canthigaster punctatissima, alizarin specimen, BC60-119, Taboga Island, Panama.

DIODONTIDAE

Branchiostegals. 6 in *Diodon* and *Chilomycterus. Chilomycterus atinga* 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform except the last, which is stout, fan-shaped, and has the upper edge elevated.
Hyoid arch. In *Chilomycterus* interhyal not seen, but epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal sutured together.
References. Chevey (1932), Fraser-Brunner (1943), Hubbs (1920), Tyler (1962).
Material examined. Chilomycterus atinga, alizarin specimen, NMC62-75 & S, North Carolina.

Suborder **Ostracioidei**

OSTRACIIDAE (ARACANIDAE)

Branchiostegals. 6 in *Ostracion, Lactophrys,* and *Rhineosomus. Rhineosomus* *triqueter* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform, the lowest not expanded. *Lactophrys tricornis* 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, upper 2 and the lowest normal acinaciform in shape, the middle 3 with rounded ends.

Hyoid arch. Short and broad in *Lactophrys* and *Rhineosomus*. In *Rhineosomus* consists of interhyal, epihyal, ceratohyal, and two hypohyals, the upper hypohyal posteriormost and partly overlying the end of the ceratohyal.

References. Day (1875), Hubbs (1920).

Material examined. Rhineosomus triqueter, alizarin specimen, NMC60-338, Barbados; *Lactophrys tricornis*, alizarin specimen, Sonda de Campeche, Mexico.

Suborder Moloidei

MOLIDAE

Branchiostegals. 6 in *Mola*; 5 in *Ranzania laevis*, the upper 2 rays being coalesced; *Mola mola* 6 with 2 epihyal and 4 ceratohyal, 4 external and 2 ventral, becoming broad distally but thick; the lowest being half as thick as wide.

Hyoid arch. In *Mola* at least epihyal, ceratohyal, and two hypohyals present, all separated by a layer of cartilage. The bones themselves are poorly ossified.

References. Fraser-Brunner (1951), Gregory (1933), Smitt (1895), Tyler (1962).

Material examined. Mola mola, alcoholic specimen, BC62-355, San Juan Harbor, Wash.

Order MASTACEMBELIFORMES[1] (CHAUDHURIIFORMES)

Pl. 21

Branchiostegals 6 with 1–1½ epihyal and 4½–5 ceratohyal, 4 on the external, the fifth on the internal, and the sixth on the ventral, all acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present. Epihyal and ceratohyal sutured. Ceratohyal without beryciform foramen. Opercular bones complete and entire, operculum suspended from above. Gill membranes separate or narrowly united and free; opening restricted from above, the opercular having no free edge. Fossils unknown. Two families.

Boulenger (1904) considered that the Mastacembelidae were possibly derived from the Blenniidae. Regan (1912) considered that they were related to but more specialized than the Percomorphi, showing no particular affinity to any one group of Percomorphous fishes. Job (1941) concluded that the larvae are percoid in appearance and that the Mastacembelidae may have originated from a percoid fish remotely allied to Nandidae. Freihofer (1963) suggested that the pattern of the ramus lateralis accessorius points to an affinity with the percoids.

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[1] The ordinal name is based on the family name which is based on the generic name. *Mastacembelus* Gronovius 1763 is unavailable. *Mastocembelus* Scopoli 1777 is the next usage. Sufi (1956) regards the substitution of an "o" for the second "a" as a slip or error in taking it from Gronovius. If this is so, *Mastacembelus*, Mastacembelidae, and Mastacembeliformes would stand (rather than the *Mastocembelus*, Mastocembelidae, and Mastocembeliformes used by Misra (1962).)

The number, arrangement, and form of the branchiostegals and the suturing of the epihyal and ceratohyal are typically acanthopterygian, and there can be little doubt, as other characters attest, that the Mastacembeliformes are derived from the Perciformes. Regan (1919) and Anandale and Hora (1923) agree that the Chaudhuriidae are related to the Mastacembelidae. With this group of related families I should like to associate the Synbranchidae. The Synbranchidae, Mastacembelidae, and Chaudhuriidae share a similar number of branchiostegals and the arrangement of the hypohyals, with the second hypohyal perforated and dorsal to the end of the ceratohyal.

These three groups, Mastacembelidae, Chaudhuriidae, and Synbranchiformes, also share the following characters: gill opening restricted from above (an unusual condition; gill openings generally are restricted from below); 70 or more vertebrae; 0–2 pelvic rays; scales cycloid or absent; gas bladder physoclistic or absent; air breathing (Chaudhuriidae not known); upper jaw nonprotrusible; no opisthotic, supramaxillary, orbitosphenoid, subocular shelf; epiotic, sphenotic, and parietals present; suborbitals reduced or absent; caudal reduced to ten or fewer rays; dorsal and anal fins and body long. The dorsal restriction of the gill opening may be associated with retention of inhaled air bubbles.

Various authors have concluded that the Synbranchidae are related to the eels, apparently considering only their external appearance. Even Bertin and Arambourg (1958) retain them in adjacent orders. The condition of the branchiostegals and the hyoid arch strongly contradicts this and indicates placement amongst the acanthopterygians.

The characters differentiating Mastacembelidae from Chaudhuriidae are few: Chaudhuriidae lack scales, fleshy tentacle on snout, and fin spines; and they have a reduced shoulder girdle and fewer vertebrae (Annandale and Hora, 1923). The Mastacembelidae are now known, like the Chaudhuriidae, to possess a basisphenoid (Sufi, 1956). Most differences may be regarded as degenerative changes. Whereas these differences certainly justify recognition of a family or possibly even a suborder, they do not appear to warrant ordinal recognition of the Chaudhuriidae. Since there are no striking characters peculiar to the Chaudhuriidae, Bailey (1960) is followed in synonymizing the order Chaudhuriiformes with the Mastacembeliformes.

MASTACEMBELIDAE

Pl. 21

Branchiostegals. 6 in *Mastacembelus* and *Macrognathus. Macrognathus aculeatus* 6 with 1½ epihyal and 4½ ceratohyal, 4 external and 2 ventral, all slender acinaciform; *M. armatus* 6 with 1½ epihyal and 4½ ceratohyal, 4 external, the fifth on the internal, and the sixth on the ventral face of the arch, all acinaciform; *M. mellandi* 6 with 1 epihyal and 5 ceratohyal, 4 external, the fifth on the internal, and the sixth on the ventral face of the hyoid arch, all acinaciform. The innermost branchiostegals of each side do not cross. *Mastacembelus pancelas* 6 with 4 external and 2 on the internal face of arch.

Hyoid arch. In *Mastacembelus* consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal joined by two or three suturing prongs. First hypohyal anteriormost, sending a small prong below ceratohyal. Second hypohyal perforated by a small foramen, with posterior two-thirds lying above the end of the ceratohyal.
References. Day (1875), Gregory (1933), Job (1941), Khanna (1961), Regan (1912), Sufi (1956).
Material examined. Mastacembelus pancelas, BC55-64, India; *Macrognathus armatus*, alizarin specimen, NMC62-207-S, India; *M. aculeatus*, BC alizarin specimen, Malaya; *M. mellandi*, alizarin specimen, NMC63-69 & S. Northern Rhodesia.

CHAUDHURIIDAE

Pl. 21

Branchiostegals. 6 in *Chaudhuria caudata* (both sides), with 1 epihyal and 5 ceratohyal, 4 external and 2 internal (the 5th inserted higher on the inner face than the 6th), all slender acinaciform.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal not sutured (specimen may be too small for this to have developed). First hypohyal anteriormost, sending a small prong below the ceratohyal. Second hypohyal lying half over the ceratohyal and half over the first hypohyal and emitting a small dorsal projection.
References. Annandale and Hora (1923), Regan (1919).
Material examined. Chaudhuria caudata, NMC63-118-S, alizarin specimen, Inle Lake, South Shan States, Burma.

Order **SYNBRANCHIFORMES (SYMBRANCHIFORMES, ALABIFORMES)**

Pl. 21

Branchiostegals 3–6 with 1–3 epihyal and 2–4 ceratohyal, 3–4 external and 0–2 ventral, acinaciform, rather stout, round in cross-section, needle-like and slightly curved; interhyal, epihyal, ceratohyal, and (one?) or two hypohyals present, the last three or four sutured together. No beryciform foramen. Opercular bones complete and entire. Gill membranes united and free, the opening restricted dorsally, resulting in a single median, ventral, oval gill opening. Fossils unknown. Three families.

Suborder **Alabetoidei**

ALABETIDAE

Branchiostegals. 3 in *Alabes rufus* with 1 epihyal and 2 ceratohyal, all external, acinaciform, needle-like, stout, and somewhat turned-down at distal end.
Hyoid arch. Consists of stout anvil-shaped interhyal, epihyal, ceratohyal, and a hypohyal which overlays the anterior end of the ceratohyal. The hypohyal would appear to have been formed through fusion of the upper and lower hypohyals. The epihyal and ceratohyal are sutured together.

Reference. Regan (1912*c*).
Material examined. Alabes rufus, alizarin specimen, NMC64-740, South Australia.

Suborder **Synbranchoidei**

CUCHIIDAE (AMPHIPNOIDAE)

Branchiostegals. 6 in *Cuchia cuchia.*
Reference. Day (1875).
Material examined. None.

SYNBRANCHIDAE (SYMBRANCHIDAE)

Pl. 21

Branchiostegals. 6 in *Synbranchus* and *Monopterus. Synbranchus marmoratus* 6 with 2–2½ epihyal and 3½–4 ceratohyal, 4 external and 2 ventral, acinaciform and stout; the anteriormost branchiostegal on the left crosses the anteriormost on the right hyoid arch; this may serve to strengthen the united gill membranes (a similar adaptation occurs in some Pleuronectiformes). *Monopterus javensis, M. bengalensis,* and *M. albus* with 6, although according to Day (1875) *javensis* may have 5 or 6. *M. albus* 6 with 3 epihyal and 3 ceratohyal, 4 external and 2 ventral needle-shaped, round in cross-section and gently curved; the upper four are short and separated from the larger two below. *M. fluta* 5, needle-like, slightly curved, the anterior one longer and not crossing its counterpart of the other side.
Hyoid arch. In *Synbranchus* interhyal, epihyal, ceratohyal, and two hypohyals present; the epihyal and the ceratohyal, the lower hypohyal and the ceratohyal firmly sutured together. In *Monopterus* epihyal and ceratohyal sutured together.
References. Chevey (1932), Day (1875), Hubbs (1920).
Material examined. Synbranchus marmoratus, alizarin specimen, NMC62-69 & S, Guatemala; alizarin preparation of arch and branchiostegals, SU 47046, Trinidad; *Monopterus albus,* skeleton, USNM 191144, Taiwan; *Monopterus fluta,* alcoholic specimen, BC58-572, Malaya.

Order **LOPHIIFORMES**

Pl. 21

Branchiostegals (4)5–6 with 0–1(2) epihyal and 5–6 ceratohyal, 4 external and 1–2 internal or ventral, all acinaciform, stout, and mesially round. Interhyal, epihyal, ceratohyal, and one or two hypohyals present. Epihyal and ceratohyal sutured or not. Ceratohyal without beryciform foramen. Opercular bones complete; operculum typically Y-shaped, often with posterior spine. Gill opening restricted. Eocene to present. Fifteen families.

The relationship of this family is discussed under Gobiesociformes where it is shown that the Lophiiformes, Batrachoidiformes, and Gobiesociformes are apparently closely related. It is likely that one of the Percoidei, or at least one of the Perciformes, gave rise to the Lophiiformes themselves.

Suborder **Lophioidei**

LOPHIIDAE

Branchiostegals. 6 in *Lophius* and *Lophiomus*. *Lophius piscatorius* 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 internal all basally stout, mesially tending to be cylindrical and terminally attenuate, acinaciform. *Chirolophius forbesii* 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral. In the deeper water forms there is a tendency for the second hypohyal, the brace between the epihyal and ceratohyal, and the spine on the suboperculum to be lost.

Hyoid arch. In *Lophius* consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal elongate, the first turned upwards at its posterior end; the two joined by interdigitating prongs dorsally. A small lower hypohyal. The larger dorsal hypohyal sends a curved lamina posteriorly along the upper and internal face of the ceratohyal where it is received by a depression in the ceratohyal. Although this projection does not have the exact form of that found in the batrachoidids and gobiesocids it will be seen that a slight lateral rotation will complete a cylinder and bring it to lie on the external face as in those two groups. *Chirolophius* similar but upper hypohyal exposed on lateral surface.

References. Garman (1899), Gregory (1933), Hubbs (1920), Jordan and Evermann (1898), Smitt (1892).

Material examined. Lophius piscatorius, alizarin specimen, NMC62-56, Emerald Bank, off Nova Scotia; *Chirolophius forbesii*, alizarin specimen, BC59-247, Mazatlan, Mexico.

Suborder **Antennarioidei**

ANTENNARIIDAE

Pl. 21

Branchiostegals. 6 in *Antennarius* and *Histrio*. *A. drombus* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform, first the stoutest.

Hyoid arch. Interhyal, epihyal, ceratohyal, and two hypohyals present.

References. Day (1875), Gregory (1933), Hubbs (1920), Jordan and Evermann (1898), Schultz (1957), Smitt (1892).

Material examined. Antennarius drombus, alizarin specimen, NMC63-120-S, Hawaii.

CHAUNACIDAE

Branchiostegals. 6 in *Chaunax coloratus* with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform.

Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and one apparently cartilaginous hypohyal (according to figure); epihyal and ceratohyal seemingly separate.

Reference. Garman (1899).

Material examined. None.

BRACHIONICHTHYIDAE

Branchiostegals. No data available.
References. Cuvier (1817), Günther (1861), MacLeay (1881).
Material examined. None.

OGCOCEPHALIDAE (ONCOCEPHALIDAE)

Branchiostegals. Vary from 5–6. *Ogcocephalus* 6, *Zalieutes* 6, *Halieutaea* 5–6, *Dibranchus* 6, *Malthopsis* 6. *Ogcocephalus darwini* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, the uppermost enlarged, all acinaciform (Hubbs, 1958, in a *lapsus calumni,* reports the posterior 4 on the epihyal). *Zalieutes elater* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 internal, all acinaciform, the uppermost notably larger and angled more vertically. *Malthopsis spinulosa* 6 with 4 external and 2 ventral, the uppermost notably larger. *Ogcocephalus vespertilio* 6, the upper 4 external, the lower 2 ventral, the upper branchiostegal greatly enlarged.
Hyoid arch. In *Zalieutes* interhyal, epihyal, ceratohyal known to be present; the epihyal and ceratohyal sutured internally and externally.
References. Day (1875), Garman (1899), Hubbs (1920, 1958), Jordan and Evermann (1898).
Material examined. Zalieutes elater, alizarin specimen, BC59-247, Mazatlan, Mexico; *Ogcocephalus darwini,* alcoholic specimen, BC56-440, Tagus Cove, Albermale Island, Galapagos Islands.

Suborder **Ceratioidei**

CAULOPHRYNIDAE

Branchiostegals. Caulophryne jordani 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform; the upper ones lie free between the epihyal and ceratohyal (the bones have not completed development in the larval skeleton portrayed, but the above would seem the most likely resulting arrangement in the adult).
Hyoid arch. In *Caulophryne* interhyal, epihyal, ceratohyal, and one hypohyal known. Epihyal and ceratohyal separate.
Reference. Bertelsen (1951).
Material examined. None.

MELANOCETIDAE

Branchiostegals. Melanocetus johnsoni 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform.
Hyoid arch. Interhyal, epihyal, ceratohyal figured. Epihyal and ceratohyal separate.
Reference. Bertelsen (1951).
Material examined. None.

HIMANTOLOPHIDAE

Branchiostegals. Himantolophus groenlandicus 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral or internal, all acinaciform.

Hyoid arch. Interhyal, epihyal, and ceratohyal figured.
References. Bertelsen (1951).
Material examined. None.

DICERATIIDAE

Branchiostegals. Diceratias bispinosus 6 with 0 or 1 on the epihyal and 5 or 6 on the ceratohyal, 4 external and 2 internal or ventral, all acinaciform. *Paroneirodes* 6.
Hyoid arch. In *Diceratias* consists of interhyal, epihyal, ceratohyal (the hypohyals not figured).
References. Bertelsen (1951), Maul (1962*a*).
Material examined. None.

ONEIRODIDAE

Branchiostegals. 6 in *Oneirodes, Lasiognathus, Thaumanichthys,* and *Chaenophryne. Chaenophryne draco* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform. *Oneirodes eschrichti* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral or internal, all acinaciform. *Lasiognathus* sp. 6 with 0 epihyal, 6 ceratohyal, 4 external and 2 ventral or internal. *Thaumanichthys pagidostomus* (?) 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform. *Dolopichthys allector* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform.
Hyoid arch. Consists of interhyal, epihyal, and ceratohyal in *Chaenophryne* and *Oneirodes*; hypohyal(s) not portrayed; epihyal and ceratohyal separate. In *Thaumanichthys* interhyal, epihyal, ceratohyal, and single hypohyal present; epihyal and ceratohyal separate.
References. Bertelsen (1951), Garman (1899), Gregory (1933), Maul (1961, 1962*a*).
Material examined. None.

CENTROPHRYNIDAE

Branchiostegals. Centrophryne spinulosa 6 with 0 or 1 epihyal and 5 or 6 ceratohyal, 4 external and 2 ventral, all acinaciform.
Hyoid arch. Consists of interhyal, epihyal, ceratohyal, and a single hypohyal; epihyal and ceratohyal separate.
Reference. Bertelsen (1951).
Material examined. None.

CERATIIDAE

Branchiostegals. 6 in *Ceratias* and *Cryptosaras. Cryptosaras couesii* and *Ceratias holboelli* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform.
Hyoid arch. In *Cryptosaras* and *Ceratias* interhyal, epihyal, ceratohyal, and two hypohyals present; epihyal and ceratohyal separate.
Reference. Bertelsen (1951).
Material examined. None.

GIGANTACTINIDAE

Branchiostegals. 6 in *Gigantactis* and *Rhynchactis. Gigantactis* 6 with 0 or 1 epihyal and 5 or 6 ceratohyal, 4 external and 2 ventral, all acinaciform.
Hyoid arch. Consists of at least interhyal, epihyal, and ceratohyal; epihyal and ceratohyal separate.
Reference. Bertelsen (1951).
Material examined. None.

NEOCERATIIDAE

Branchiostegals. Neoceratias spinifer 5–6 with 4 external and 2 ventral or internal, all acinaciform.
Hyoid arch. Consists of interhyal, epihyal, and ceratohyal; epihyal and ceratohyal separate; hypohyals not portrayed.
Reference. Bertelsen (1951).
Material examined. None.

LINOPHRYNIDAE

Branchiostegals. Usually 5, rarely 4. *Photocorynus spiniceps, Edriolychnus schmidti, Linophryne macrophryne,* and *Borophryne apogon* 5, all on the ceratohyal, with 4 external and 1 ventral or internal, all acinaciform. *Linophryne coronata* 5 with 1 epihyal and 4 ceratohyal, 4 external and 1 ventral.
Hyoid arch. In *Photocorynus* and *Borophryne* consists of interhyal, separate epihyal and ceratohyal, and a single hypohyal; similar in *Edriolychnus* and *Linophryne* except hypohyal not exhibited in figure. The hyoid barbel was not supported by branchiostegals.
Reference. Bertelsen (1951).
Material examined. Linophryne coronata, SIO-282-65A, from 27°05′ N, 138° 25′ W to 27°15.5′ N, 137°58′ W.

Order BATRACHOIDIFORMES
Pl. 21

Branchiostegals 6 with 2 epihyal and 4 ceratohyal, 4 external and 2 internal or ventral, all acinaciform, tending to be round in section mesially. Two hypohyals, the upper sending a cylindrical projection along the dorso-lateral face of the ceratohyal; the upper hypohyal with a foramen. Ceratohyal, epihyal, and interhyal present; ceratohyal and epihyal sutured. Ceratohyal without beryciform foramen. Opercular bones complete, opercular with one or two spines. Gill membranes broadly joined to isthmus. Pliocene to present. A single family.

The relationships of this family are discussed under Gobiesociformes—that they were derived from forms close to the Lophiiformes and that the close ancestors of the Batrachoidiformes gave rise to the Gobiesocidae. Starks (1923), however, believed that the batrachoids were allied to the uranoscopoids.

BATRACHOIDIDAE

Pl. 21

Branchiostegals. 6 in *Coryzichthys, Holobatrachus, Opsanus,* and *Porichthys. P. notatus* (two specimens) 6 with 2 epihyal and 4 ceratohyal, 4 upper ones external, the next one internal, and the lowest one ventral, all acinaciform.

Hyoid arch. In *Porichthys* consists of interhyal, epihyal, ceratohyal, and two hypohyals. Epihyal and ceratohyal sutured. The upper hypohyal sends a cylindrical projection along the dorsolateral face of the ceratohyal, which has a groove to receive it. A foramen is located in the upper corner of the upper hypohyal. The anteriorly placed lower hypohyal sends one prong obliquely postero-ventrally and a second smaller prong between the upper hypohyal and the end of the ceratohyal.

References. Day (1875), Fowler (1936), Hubbs (1920), Jordan and Evermann (1898), Meek and Hildebrand (1928), Smitt (1892).

Material examined. Porichthys notatus, alizarin specimen, BC53-302, Denman Island, B.C.; alizarin specimen, NMC59-99, English Bay, B.C.

Order GOBIESOCIFORMES

Pl. 21

Branchiostegals 5–7, usually 6, with 2 epihyal and 4 ceratohyal, 4 external and 2 internal, all stout and acinaciform. One hypohyal, ceratohyal, epihyal, and interhyal present. Hypohyal sending a cylindrical extension along the dorsolateral face of the ceratohyal. Ceratohyal and epihyal separate. Without beryciform foramen. Opercular bones complete; posterior borders of operculum and suboperculum may be fimbriated and the latter may terminate in a spine. Gill membranes united and free from isthmus or joined to isthmus. There is a possible Miocene fossil (*Bulbiceps*). A single family.

Among the various opinions expressed as to the origins of the Gobiesocidae, Boulenger (1904) has suggested the Callionymidae because of the position of the pelvic fins; Starks (1905), after a careful osteological study of it and related groups, came up with "small results" although the families Batrachoididae and Callionymidae, particularly the first, did offer some slight indications of relationship. Regan (1929) suggested only that they were related to the Percomorphi; Briggs (1955) stated that they were most closely allied to the batrachoids but said that there was some resemblance to the Callionymoidei; Freihofer (1963) considered the pattern of the ramus lateralis accessorius to be basically like the pattern in Cottidae and Liparidae.

The branchiostegal number, shape, and arrangement confirm that the Gobiesocidae are acanthopterygian. That the epihyal and ceratohyal are separate must be regarded as a secondary condition. The stout and mesially cylindrical branchiostegals are similar to those in Batrachoidiformes and Lophiiformes (ordinarily acanthopterygian branchiostegals are flatter in cross-section). As in the Batrachoididae, the fifth branchiostegal is more dorsally inserted on the mesial face and the branchiostegals increase in size downwards, except that the third is largest in Gobiesocidae and the fourth in Batrachoididae; the size then decreases downwards from the largest. A most striking similarity exists between the single hypohyal of the Gobiesocidae and the upper hypohyal of the Batrachoididae. In both, the body of the hypohyal is cylindrical and lies projecting outwards along the external face of the ceratohyal; the ceratohyal is slightly hollowed out to receive the hypohyal; between the posterior end of the hypohyal and the ceratohyal is a slight gap, then there is a socket on the ceratohyal to receive this end; the upper anterior end of the hypohyal has a projection and there is a small foramen on the anterior end of the hypohyal. These hypohyal and ceratohyal characters are not known together in any other group. Although the Gobiesociformes have only one hypohyal, its ventral anterior corner resembles the lower hypohyal of the Batrachoididae; it requires little imagination to consider that the single hypohyal of Gobiesocidae is the result of fusion of the two, and the loss of the ventral posteriorly directed prong of the lower hypohyal in Batrachoididae. It remains to be seen whether embryology will provide evidence for the latter. In a 10-mm (standard length) specimen there was only one hypohyal with no sign of a fusion. Unfortunately, Runyan (1961), who studied the embryology of *Gobiesox strumosus*, does not dwell upon this point. The condition of the hyoid arch in the Lophiidae also resembles that of Gobiesocidae, but to a lesser extent.

Examination of the caudal skeletons of *Gobiesox* and *Porichthys* showed them to be very similar. Both have two hypural plates each bearing six fin rays. The lower hypural in each sends forward a projection on the lower side. The fin rays emit a small lateral projection where they contact the hypurals. In addition, the last neural and haemal arches are slightly expanded terminally instead of being attenuate.

Other characters the Gobiesocidae shares with the Batrachoididae include the following: branchiostegals usually 6; gill membranes may be joined to the isthmus; number of gills reduced from 4; similar vertebral range; ventral fin rays reduced; apparently only epipleural ribs present; infraorbitals and spinous dorsal reduced or absent; posttemporal simple; without opisthotic, pterosphenoid, or basisphenoid; pelvics anterior; dorsal reduced or absent; branched caudal rays 10 or less. These characters are also shared with the Lophiiformes except that in the Lophiiformes the pelvics have 5 soft rays and the epipleurals are absent. At least the primitive Lophiiformes have similar hyoid arches. Thus, the Lophiiformes, although slightly more primitive, can be judged to belong to this group of orders. Although they are more primitive than the Batrachoidiformes and the Batrachoidiformes are more primitive than the Gobiesociformes, neither is directly ancestral to the other, each group having its own specializations. But it seems likely that the Lophiiformes are closest to the ancestral form, that the Batrachoidiformes arose fairly close to the branching off point of the Lophiiformes, and that the Gobiesociformes are fairly close to the branching off point of the Batrachoidiformes.

GOBIESOCIDAE

Pl. 21

Branchiostegals. Vary from 5–7. *Apletodon* 6, *Aspasmaminima* 6, *Aspasmichthys* 6, *Aspasmogaster* 6, *Chorisochismus* 6, *Conidens* 6, *Cochleoceps* 6, *Creocele* 6–7, *Dellichthys* 6, *Diplecogaster* 6, *Diplocrepis* 6, *Gastrocyathus* 6, *Gastroscyphus* 6, *Gobiesox* 6, *Gouania* 6, *Haplocylix* 6, *Lepadichthys* 6, *Liobranchia* apparently 6, *Opeatogenys* 5, *Parvicrepis* 5–6, *Pherallodus* 6, *Trachelochismus* 6–7. *Gobiesox maeandricus* (five specimens) 6 with 2 epihyal and 4 ceratohyal, 4 external and 2 internal, all stout and acinaciform; the central portion of the branchiostegals is nearly round in cross-section, not flat; the posteriormost of the 2 internal branchiostegals is inserted higher up on the mesial face. *Gobiesox strumosus* 6 with 4 external and 2 internal.

Hyoid arch. In *Gobiesox* consists of interhyal, epihyal, ceratohyal, and one hypohyal. Epihyal subrectangular with interhyal parallel to its posterior face and pivoting on its posterior ventral corner, an unusual relationship. The epihyal and ceratohyal are separate. The ceratohyal is elongate, the expansion at its epihyal end occupying a very small space. The ceratohyal is grooved on its dorso-lateral face to receive the cylindrical portion of the hypohyal. The anterior end of the hypohyal sends out a dorsal and ventral projection. From its appearance it seems likely that the hypohyal is composed of a fusion of the lower small batrachoid hypohyal and the larger upper one. A 10-mm specimen did not show a separate lower hypohyal or a line of fusion.

References. Briggs (1955), Runyan (1961), Starks (1905).

Material examined. Gobiesox maeandricus, two alizarin specimens, NMC62-29, Ucluelet, B.C.; alizarin specimen, NMC60-297, Roller Bay, B.C.; alizarin specimen, BC59-291, Jordan River, B.C.; skeletal specimen, USNM 26446, Monterey, California.

Order PEGASIFORMES

Pl. 21

Branchiostegals 5 with 2–3 on the epihyal and 2–3 on the ceratohyal, 4 external and 1 on the internal surface, all elongate acinaciform, curving up around parallel to gill cover. Interhyal, sutured epihyal and ceratohyal, and two hypohyals present. Ceratohyal without a beryciform foramen. Opercular bones complete and entire; operculum and suboperculum very small; interoperculum inserting on epihyal and resembling a large interhyal. Preoperculum forming a pseudogular. Gill opening restricted to small lateral pore. A single extant family.

The relationships of this extremely unusual-looking family are not clear. Jungerson (1915) considered them to be clearly acanthopterygian and to represent at least a suborder of their own, but he suggested that they might be a strongly modified offshoot from the stem of the Scleroparei. However, he admitted they showed no close relationship with existing Scleroparei and certainly not with forms such as *Agonus* or *Aspidophoroides.* Rendahl (1930) did not venture an opinion on relationships in his revision of the family. Regan in 1913 stated that the rather striking similarities to some of the Scorpaenoidei did not indicate relationship and later (1929) that the systematic position was uncertain. Berg (1947) accorded them the most advanced position in his scheme of fishes but gave no opinion on their origin. The body armour suggests relationship to the syngnathids or agonids and the pectorals suggest relationship to the dactylopterids according to Herald (1961).

The arrangement of the branchiostegals, the protrusible premaxillaries, and the spine in the ventral fin clearly indicate that this family is acanthopterygian. The unusual hyoid arch with the single hypohyal, the pseudo-interhyal, the modified opercular bones, and the gill opening reduced to a pore confirm other indications that this family is highly advanced and distinctive. The branchiostegals show some resemblance to those of the lophioids. Several other characters are shared with lophioids: horizontal pectorals, restricted gill openings, few principal caudal rays, posttemporal fused to skull, three or fewer pectoral radials, protrusible upper jaw, lack of opisthotic and basisphenoid, and reduced infraorbital series. Externally there is some resemblance to the Ogcocephalidae. However, some of these characters may well represent parallelisms.

There are certain similarities to the Indostomidae: the number of branchiostegals (5–6), the presence of bony plates on the body, the laterally spinous elongate nasals, the ventrals reduced and subabdominal, the upper jaw protrusible, the pectoral rays unbranched, the jaw teeth reduced or absent, the posttemporal joined to the skull, the branchiostegals curving up behind operculum (according to figure of *Indostomus* in Prashad and Mukerji), and the anal lying below the soft dorsal. The number of rays in the soft dorsal and anal and the number of vertebrae and body plates are about the same. The Pegasidae and the Indostomidae differ in the following ways: the Pegasidae have the first seven vertebrae joined (this is probably to support the longer snout); the caudal rays of the Pegasidae are fewer and unbranched (8 as opposed to 12); the gill membranes are joined to the isthmus in the Pegasidae but separate in *Indostomus*; the Pegasidae lack a spinous dorsal (but the supports for one exist according to Jungerson); and the Indostomidae lack a pelvic spine (according to Bolin). In all these characters, except the last, the Pegasidae are more advanced than the Indostomidae. None of the differences would appear to preclude the derivation of the Pegasiformes from the Indostomidae. The pelvic spine of the Indostomidae can be considered to have been lost. However, until the branchiostegals, hyoid arch, caudal skeleton, and other characters of the Indostomidae (and the Pegasidae) are better known, it seems advisable to leave the Indostomidae where they are. The Pegasidae are marine Indo-Pacific and the Indostomidae are freshwater Burmese fish. A marine invasion during the Tertiary is known to have occurred in the present range of the Indostomidae, however, and they may have had marine ancestors.

Another relationship is suggested by the peculiar opercular bones of the Pegasidae. The operculum and suboperculum are very small and hidden in a fold of skin behind the preoperculum. The interoperculum does not contact the suboperculum, but it is connected posteriorly to the hyoid arch; both its ends are notched. These peculiar features are found elsewhere only in the Dactylopteridae. Other shared characters would also suggest relationship: anterior vertebrae joined; similar number of vertebrae; nasals coalesced; eight caudal rays; pectorals unbranched, elongate, and horizontal, with the uppermost rays apparently forming the anterior border (whereas in the Triglidae the ventral rays form the anterior border); gill membranes joined to isthmus and opening constricted; and suborbitals attached to preoperculum. This possibility deserves further investigation.

PEGASIDAE

Pl. 21

Branchiostegals. Pegasus 5. *Pegasus volitans* 5 with 2 or 3 epihyal and 2 or 3 ceratohyal, 4 external and 1 internal, all acinaciform and very long attenuating to filiform distally, paralleling the edge of the pseudogular around behind to the gill opening.

Hyoid arch. Small interhyal inserting on internal face of epihyal; epihyal and ceratohyal stout and sutured strongly together; hypohyal sutured to anterior end of ceratohyal, hypohyal extending along the whole length of the ventral face of the ceratohyal—the latter is a unique relationship.

References. Jungerson (1915), Rendahl (1930).

Material examined. Pegasus volitans, alizarin preparation of arch and branchiostegals, SU 27700, Batanga, Luzon, Philippines; alizarin specimen, NMC63-115-S, Takao, Formosa.

TABLE 1. Comparison of Opercular Series and Hyoid Arch in Orders of Telestome Fishes.

TABLE 1. Comparison of Opercular Series and Hyoid Arch in Orders of Teleostome Fishes

+ = present
0 = absent
— = not known
s = spathiform
a = acinaciform
v = virgaform
f = filiform
( ) = rarely

Orders	Median Gulars	Pairs of Lateral Gulars	Number of Branchiostegals	Number of Branchiostegals on				Branchiostegals in 4 + X Pattern	Branchiostegal Shape	Hyoid Elements Present:				Epihyal-Ceratohyal Suture	Beryciform Foramen	Gill Membranes:			Opercular Elements Present:			
				Interhyal	Epihyal	Ceratohyal	Hypohyal			Interhyal	Epihyal	Ceratohyal	Hypohyals			Separate	United	Joined	Operculum	Suboperculum	Interoperculum	Spines on Operculars (any element)
CLASS TELEOSTOMI *SUBCLASS CROSSOPTERYGII*																						
Porolepiformes	0	1	10–13	—	—	—	—	—	s	—	—	—	—	—	—	—	—	—	+	+	0	0
Osteolepiformes	1	1	4–8	—	—	—	—	—	s	—	—	—	—	—	—	—	—	—	+	+	0	0
Coelacanthiformes	0	1	0	0	0	0	0	0	0	+	0	+	0	0	0	—	—	—	+	+	0	0
SUBCLASS DIPNEUSTI																						
Dipteriformes	1–2	2	2–3	—	—	—	—	0	s	—	—	—	—	—	—	—	—	—	+	+	0	0
Phaneropleuriformes	1	2	2	—	—	—	—	0	s	—	—	+	—	0	0	—	—	—	+	+	0	0
Uronemiformes	—	—	—	—	—	—	—	—	—	—	—	+	—	0	0	—	—	—	+	+	0	0
Ctenodontiformes	—	1+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	0	0
Ceratodiformes	0	0	0	0	0	0	0	0	0	?	0	+	1	0	0	0	0	+	+	+	0	0
Lepidosireniformes	0	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	+	+	+	0	0
SUBCLASS BRACHIOPTERYGII																						
Polypteriformes	0	1	0	0	0	0	0	0	0	+	0	+	1	0	0	+	0	0	+	+	0	0
SUBCLASS ACTINOPTERYGII CHONDROSTEI																						
Palaeonisciformes	0–1(2)	0–1	(1) 4–23	—	—	—	—	—	s	+	+	+	1	0	0	—	—	—	+	+	0	0
Tarrasiiformes	—	?	15	—	—	—	—	—	s	—	—	—	—	—	—	—	—	—	+	+	0	0
Phanerorhynchiformes	—	—	long series	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	0	0
Haplolepiformes	1	1	1–3	—	—	—	—	0	s	—	—	—	—	—	—	—	—	—	+	+	0	0
Redfieldiiformes	0	0	1–2	—	—	—	—	0	s	—	—	—	—	—	—	—	—	—	+	+	0	0
Perleidiformes	1	1	7–12	—	—	—	—	—	s	—	—	+	—	0	0	—	—	—	+	+	0	0
Dorypteriformes	0	0	0	—	—	?	—	0	0	—	—	?	—	—	—	—	—	—	?	0	0	0
Bobasatraniiformes	—	—	0–4+	—	—	—	—	—	s	—	—	+	—	0	0	—	—	—	+	0	0	0
Pycnodontiformes	0	0	2–5+	—	—	—	—	—	vs	—	—	—	—	—	—	—	—	—	+	0	0	0
Ptycholepiformes	1	—	5–11	—	—	—	—	—	s	—	—	+	1	0	0	—	—	—	+	+	0	0
Pholidopleuriformes	1	1	6–14	—	—	—	—	—	s	—	—	+	1	0	0	—	—	—	+	+	0	0
Cephaloxeniformes	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	0
Aethodontiformes	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	0
Peltopleuriformes	—	—	6–7	—	—	—	—	—	s	—	—	—	—	—	—	—	—	—	+	+	0	0
Chondrosteiformes	0	0	9–12	—	—	—	—	—	s	?	—	+	?	0	0	—	—	—	+	+	0	0
Saurichthyiformes	0	0	1–3?	—	—	—	—	0	—	—	—	+	1	0	0	—	—	—	+	0	0	0
Acipenseriformes	0	0	1	1	0	0	0	0	—	+	0	+	1	0	0	0	+	+	+	+0	0	0

TABLE 1. Comparison of Opercular Series and Hyoid Arch in Orders of Teleostome Fishes — *Continued*

HOLOSTEI																						
Ospiiformes	1–2	0	9–12	—	2	8	—	—	s	+	+	+	—	0	0	—	—	—	+	+	+	0
Platysiagiformes	1	0	13–20	—	—	—	—	—	s	—	—	—	—	—	—	—	—	—	+	+	+	0
Luganoiiformes	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	0
Amiiformes	1	0	5–30	0	0–4	10–21	0	0	s	+	+	+	1	0	0	+	0	0	+	+	+	0
Lepisosteiformes	0	0	3	0	2	1	0	0	s	?	+	+	1	0	0	0	+	0	+	+	0	0
Aspidorhynchiformes	0	0	12–13	—	—	—	—	—	s	—	—	—	—	—	—	—	—	—	+	+	+	0
Pachycormiformes	1	0	6+ – 50	0	22	20	0	—	s	—	+	+	1	0	0	—	—	—	+	+	+	0
Pholidophoriformes	1	0	1?5+ – 18+	—	—	—	—	—	s	?	+	+	—	0	0	—	—	—	+	+	+	0
Leptolepiformes	1	0	21	0	9	12	0	0	s	+	+	+	1	0	?	—	—	—	+	+	+	0
TELEOSTEI																						
MALACOPTERYGII																						
Clupeiformes	0(1)	0	1–36	0–1	½–12	0–23	0–5	0(+)	s	+(0)	+	+	(1)2	0	0	+	(+)	(+)	+	+	+	0
Notacanthiformes	0	0	6–23	0	4–7	2–7	0	0	a	+	+	+	2	0	0	+	0	0	+	+	+	0
Mormyriformes	0	0	3–17	0	0–5	1–8	0	0	av	0+	+	+	0–1	0	0	+	+	+	+	0+	+	0
Cypriniformes	0	0	3–20	0	1–3	2–13	0	0	s	+	+	+	(1)2	0+	0	+	+	+	+	0+	+	0
Anguilliformes (+ 4–46 jugostegelia)	0	0	6–22	0	4–12	0–6	0	0	f	0	+	+	0–1	0	0	0	0	+	+	(0)+	(0)+	0
Giganturiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+	+	+	0
Saccopharyngiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0
ACANTHOPTERYGII																						
Myctophiformes	0	0	6–26	0–2	2–14	3–10	0–2	+(0)	a	+	+	+	2	0	0	+	0	0	+	+	+	0
Cetomimiformes	0	0	7–10	0	3–4	4–5	0	+	a	+	+	+	2	0?	+	+	+	0	+	+	+	0
Mirapinniformes	0	0	7–9	0	3–5	4	0	+(0)	a	+	+	+	2	0	+0	+	0	0	+	+	+	0
Ctenothrissiformes	0	0	9	0	2–3½	5½–7	0	+	a	+	+	+	2	0+	+	—	—	—	+	+	+	0
Beryciformes	0	0	(5?) 7–9 (10, 12?)	0	2(3)	2–7	0(3–4)	+(0)	a	+	+	+	2	0	+(0)	+	0	0	+	+	+	+0
Lampridiformes	0	0	5–7	0	0–3	3–5	0	+(0)	a	+	+	+	1–2	0	+0	+	0	+	+	+	+	0
Zeiformes	0	0	(5) 6–8	0	0–1(4)	2–8	0	+	a	+	+	+	2	+	+	+	0	0	+	+	+	0
Syngnathiformes	0	0	1–5	0	0–4	0–4	0	0+	af	+(0)	+	+	1–2	+	0	+	0	+	+	+	+	0
Ophidiiformes	0	0	(5) 6–9 (10)	0	2	5–6	0	+	a	+	+	+	2	+	0	+	+	+	+	+	+	+0
Ateleopiformes	0	0	7–9	0	3–4	4	0	+	a	+	+	+	2	0	0	+	0	0	+	+	+	0
Gadiformes	0	0	(5) 6–8	0	0–1	5–8	0	+	a	+	+	+	2	+(0)	0	+	+	+	+	+	+	0
Percopsiformes	0	0	6(7)	0	1	5	0	+	a	+	+	+	2	+	0+	+	0	+	+	+	+	0+
Atheriniformes	0	0	4–15	0	1–4	4–9	0–3	+0	a	+	+	+	1(2)	+	0	+	+	0	+	+	+	0
Pleuronectiformes	0	0	6–7(8)	0	2–4	3½–5	0	+	a	+	+	+	2	+	0+	+	+	0	+	+	+	0
Ophicephaliformes	0	0	5–6	0	0–3	2–5	0	+	a	+	+	+	2	+	0	+	+	0	+	+	+	+0
Perciformes	0	0	(3) 4–7 (8)	0	0–4	2–6	0	+(0)	a	+	+	+	(1)2	+(0)	0(+)	+	+	+	+	+	+	+0
Gasterosteiformes	0	0	3–4	0	1	2–3	0	+0	a	+	+	+	2	+	0	0	+	+	+	+	+	0
Icosteiformes	0	0	6–7	0	1–2	4–5	0	+	a	+	+	+	2	0	0	0	0	+	+	+	+	0
Echeneiformes	0	0	8–11	0	2	6–9	0	+	a	+	+	+	2	+	0	+	0	0	+	+	+	0
Tetraodontiformes	0	0	(3)5–6	0	0–2	3½–6	0	+(0)	a	+	+	+	2	+(0)	0	0	0	+	+	+	+	0(+)
Mastacembeliformes	0	0	6	0	1–1½	4½–5	0	+	a	+	+	+	2	+	0	+	+	0	+	+	+	0
Synbranchiformes	0	0	3–6	0	1–3	2–4	0	+(0)	a	+	+	+	1–2	+	0	0	+	0	+	+	+	0
Lophiiformes	0	0	(4)5–6	0	0–1(2)	5–6	0	+	a	+	+	+	1–2	+0	0	0	0	+	+	+	+	+0
Batrachoidiformes	0	0	6	0	2	4	0	+	a	+	+	+	2	+	0	0	0	+	+	+	+	+
Gobiesociformes	0	0	5–7	0	2	4	0	0	a	+	+	+	1	0	0	0	+	+	+	+	+	0+
Pegasiformes	0	0	5	0	2–3	2–3	0	+	a	+	+	+	2	+	0	0	0	+	+	+	+	0

Review of Previous Classifications

Günther's classification, in his *Catalogue of Fishes* (1859–1870), followed Cuvier and Valenciennes quite closely. Using few features to characterize his major taxa, he employed 3 subclasses but only 8(+1) orders and 78 families.

Regan's (1929) classification (*see Table* 2) was a notable advance over previous haphazard assemblages. He had a keen eye for differences and a compact style of description. His classification was based largely on his own studies of the osteology of the different orders; often only a single representative of a group was studied. Fossil groups received little attention.

Berg (1940–1947) gave more attention to fossil groups. His encyclopedic knowledge of the anatomical literature enabled him to give superior definitions to taxa. It has been suggested that much of his classification derived from the studies of Woodward and Regan, but there is no doubt that his own contributions were substantial. He was himself active in palaeoichthyology and neoichthyology. Although his classification was generally balanced he may have overemphasized the importance of some structures (e.g., of the olfactory lobes in the recognition of the orders Galaxiiformes and Macruriformes). Rather than emend the supraordinal groupings—Chondrostei, Holostei, and Teleostei—he discarded them, which, holus-bolus, many recent ichthyologists have followed. Probably Berg's greatest contribution was in the integration of numerous anatomical and biological features to form an expanded classification. He was more complete in the inclusion of families than were the following two studies, but he raised some groups to ordinal status that were not highly distinguished. Briggs has pointed out Berg's erroneous use of emended names,[1] but perhaps error is unavoidable in a work of such scope.

Romer's (1955) classification of fishes was not included in the table because it was based on little new research. Nevertheless, his classification is quite different; only 17 orders are recognized (even Regan recognized 38 orders). Also, Romer's order Mesichthyes is a polymorphic catch-all group, and the subclass Choanichthyes is invalid (see *Traité de Zoologie*) since the Dipnoi do not have true internal nostrils.

Bertin, Lehman, Arambourg, and others have contributed to the classification of bony fishes in the *Traité de Zoologie* (1958). This study is freely illustrated and it provides a greater emphasis on biology. It elevates many lesser groups to ordinal rank, some of which are little known and not well characterized (Cephaloxeniformes, Aethodontiformes, Luganoiformes, only provisionally accepted here). A number of families have been overlooked. The already diverse order Clupeiformes has had further taxa added to it. A number of generally accepted orders have been lumped with the Perciformes

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[1] But Lindberg (1963) disputes Briggs's suggestion that Berg was in error. Zool. Zhur. 42(7): 1105–1107.

TABLE 2. Evolution of the Classification of Teleostome Fishes

REGAN 1929	BERG 1940	BERTIN and ARAMBOURG 1958	McALLISTER 1967
CLASS PISCES	CLASS DIPNOI	CLASS OSTEICHTHYES	CLASS TELEOSTOMI
SUBCLASS CROSSOPTERYGII	*SUPERORDER DIPTERI*	*SUBCLASS BRACHIOPTERYGII*[1]	*SUBCLASS CROSSOPTERYGII*
Rhipidistia	Dipteriformes	Polypteriformes	Porolepiformes
Actinistia	Rhynchodipteriformes	*SUBCLASS PIPNEUSTI*[1]	Osteolepiformes
Dipneusti	Phaneropleuriformes	SUPERORDER DIPTERI	SUPERORDER COELACANTHI
	Uronemiformes	Dipteriformes	Coelacanthiformes
SUBCLASS PALAEOPTERYGII	Ctenodontiformes	Phaneropleuriformes	*SUBCLASS DIPNEUSTI*
Archistia	SUPERORDER CERATODI	Ctenodontiformes	SUPERORDER DIPTERI
Belonorhynchii	Ceratodiformes	SUPERORDER CERATODI	Dipteriformes
Chondrostei	Lepidosireniformes	Ceratodiformes	Phaneropleuriformes
Cladistia		*SUBCLASS CROSSOPTERYGII*[1]	Uronemiformes
	CLASS TELEOSTOMI	SUPERORDER RHIPIDISTII	Ctenodontiformes
SUBCLASS NEOPTERYGII	*SUBCLASS CROSSOPTERYGII*	Osteolepiformes	SUPERORDER CERATODI
Protospondyli	SUPERORDER OSTEOLEPIDES	Porolepiformes	Ceratodiformes
Ginglymodi	Osteolepiformes	SUPERORDER ACTINISTII	Lepidosireniformes
Halecostomi	Hoploptychiformes	Coelacanthiformes	*SUBCLASS BRACHIOPTERYGII*
Isospondyli	Rhizodontiformes	*SUBCLASS ACTINOPTERYGII*	Polypteriformes
Haplomi	SUPERORDER COELACANTHI	SUPERORDER CHONDROSTEI	*SUBCLASS ACTINOPTERYGII*
Iniomi	Coelacanthiformes	Tarrasiiformes	CHONDROSTEI
Giganturoidea	*SUBCLASS ACTINOPTERYGII*	Palaeonisciformes	Palaeonisciformes
Lyomeri	GROUP A	Dorypteriformes	Tarrasiiformes
Ostariophysi	Polypteriformes	Bobasatraniiformes	Phanerorhynchiformes
Apodes		Haplolepiformes	Haplolepiformes
Heteromi	GROUP B	Aeduelliformes	Redfieldiiformes
Synentognathi	Tarrasiiformes	Pholidopleuriformes	Perleidiformes
Microcyprini	Palaeonisciformes	Perleidiformes	Dorypteriformes
Salmopercae	Gymnonisciformes	Luganoiiformes	Bobasatraniiformes
Solenichthyes	Phanerorhynchiformes	Ptycholepiformes	Pycnodontiformes
Anacanthini	Dorypteriformes	Ospiiformes	Ptycholepiformes
Allotriognathi	Bobasatraniiformes	Phanerorhynchiformes	Pholidopleuriformes
Berycomorphi	Redfieldiiformes	Saurichthyiformes	Cephaloxeniformes
Zeomorphi	Perleidiformes	Chondrosteiformes	Aethodontiformes
Percomorphi	Ospiiformes	Acipenseriformes	Peltopleuriformes
Scleroparei	Pholidopleuriformes		Chondrosteiformes
Hypostomides	Saurichthyiformes	SUPERORDER HOLOSTEI	Saurichthyiformes
Heterosomata	Acipenseriformes	Semionotiformes	Acipenseriformes
Discocephali	Amiiformes	Amiiformes	HOLOSTEI
Plectognathi	Aspidorhynchiformes	SUPERORDER HALECOSTOMI	Ospiiformes
Malacichthyes	Pycnodontiformes	Pholidophoriformes	Luganoiiformes
Xenopterygii	Pachycormiformes	Leptolepiformes	Platysiagiformes
Haplodici	Lepidosteiformes	Aspidorhynchiformes	Amiiformes
Pediculati	Pholidophoriformes	SUPERORDER TELEOSTEI	Lepisosteiformes
Opisthomi	Clupeiformes	Clupeiformes	Aspidorhynchiformes
Symbranchii	Bathyclupeiformes	Tetraodontiformes	Pachycormiformes
	Galaxiiformes	Cypriniformes	Pholidophoriformes
	Scopeliformes	Anguilliformes	Leptolepiformes
	Ateleopiformes	Synbranchiformes	
	Giganturiformes	Alabiformes	

TABLE 2. Evolution of the Classification of Teleostome Fishes — *Continued*

REGAN 1929	BERG 1940	BERTIN and ARMBOURG 1958	McALLISTER 1967
CLASS PISCES	CLASS TELEOSTOMI	CLASS OSTEICHTHYES	CLASS TELEOSTOMI
	Saccopharyngiformes	Giganturiformes	TELEOSTEI
	Mormyriformes	Saccopharyngiformes	*Malacopterygii*
	Cypriniformes	Monognathiformes	Clupeiformes
	Anguilliformes	Bathyclupeiformes	Notacanthiformes
	Halosauriformes	Percopsiformes	Mormyriformes
	Notacanthiformes	Notacanthiformes	Cypriniformes
	Beloniformes	Beloniformes	Anguilliformes
	Gadiformes	Gasterosteiformes	Giganturiformes
	Macruriformes	Aulostomiformes	Saccopharyngiformes
	Gasterosteiformes	Syngnathiformes	*Acanthopterygii*
	Syngnathiformes	Cyprinodontiformes	Myctophiformes
	Lampridiformes	Amblyopsiformes	Cetomimiformes
	Cyprinodontiformes	Phallostethiformes	Mirapinniformes
	Phallostethiformes	Mugiliformes	Ctenothrissiformes
	Percopsiformes	Polynemiformes	Beryciformes
	Stephanoberyciformes	Gadiformes	Lampridiformes
	Beryciformes	Lampridiformes	Zeiformes
	Zeiformes	Stephanoberyciformes	Syngnathiformes
	Mugiliformes	Beryciformes	Ophidiiformes, n. order
	Polynemiformes	Zeiformes	Ateleopiformes
	Ophiocephaliformes	Coryphaeniformes	Gadiformes
	Symbranchiformes	Perciformes	Percopsiformes
	Perciformes	Pleuronectiformes	Atheriniformes
	Dactylopteriformes	Mastacembeliformes	Pleuronectiformes
	Thunniformes	Lophiiformes	Opicephaliformes
	Pleuronectiformes		Perciformes
	Icosteiformes		Gasterosteiformes
	Chaudhuriiformes		Icosteiformes
	Mastacembeliformes		Echeneiformes
	Echeneiformes		Tetraodontiformes
	Tetrodontiformes		Mastacembeliformes
	Gobiesociformes		Synbranchiformes
	Batrachoidiformes		Lophiiformes
	Lophiiformes		Batrachoidiformes
	Pegasiformes		Gobiesociformes
			Pegasiformes
No. subclasses			
3	2 + 1 class	4	4
No. supraordinal groups			
0	6	8	9
No. of orders of Teleostomes			
38	71	59	66 + 3
No. of orders of Teleostei			
28	41	31	33

[1] Moved from the bottom to the top of the classification to facilitate comparison.

(only 3 post-perciform orders are recognized as compared to 12 in Berg). However, the authors have retained the superorders discarded by Berg, with little change in the constitution, and recognize in addition the superorder Halecostomi. Some parallel evolution has not been recognized. Valuable material in *Latimeria chalumnae* is included.

A valuable contribution to classification, a paper by Greenwood, Rosen, Weitzman, and Myers (Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131:339–456. 4 pl., 9 text-fig.), was received while the present study was in press. Their classification is not included in Table 2 since it covers only the living forms of teleosts, omitting the lower Actinopterygii and the other three subclasses of teleostomes. New and interesting relationships and characters are presented. A more detailed break-down of the teleosts at the superordinal level, long needed, is provided. Many firm characters are employed. Unfortunately these characters are not consistently compared even in neighbouring groups. This makes it difficult to evaluate the classification and to utilize the characters in other studies. A polyphyletic origin is shown for their Paracanthopterygii and Acanthopterygii. Their classification and the present one are to a considerable extent complementary, although there are points in both that will have to be modified. They include thirty orders.

The present study attempts to summarize current advances in taxonomy. Some modifications in classification suggested by the study and confirmed by other structures are integrated into the classification. An attempt is made to achieve a balance between lumping and splitting. However, some of the recently named fossil orders provisionally accepted herein (*see* above paragraph) may need to be synonymized with other orders. The chief changes, perhaps, are in the diagnoses of supraordinal groups, in the realignment of several orders, and in the more sharply defined suggestions as to origin of several groups. However, the final position of several orders within their superorders remains yet to be determined. Many of the fossil orders are in need of revision (e.g., Amiiformes, Palaeonisciformes).

In constructing classifications several points should be kept in mind. Changes should be made on the basis of new information with an awareness of the frequency of parallel evolution in fishes. Data from fossils should be used as much as possible. Classification should be based on as many firm systematic characters as possible, including biological as well as morphological characters. These should be investigated, described (in standard format), and analysed throughout the supertaxa to which they are pertinent.

Summary and Conclusions

1. The structure and arrangement of branchiostegals, operculars, gulars, and lower elements of the hyoid arch were studied in the class Teleostomi. The branchiostegals of at least one specimen of more than 245 families of teleostomes were examined. Alizarin, skeletal, and alcoholic specimens were utilized. Data for these and most of the remaining families were also obtained from the literature. Fossil taxa were included in the study, but data for these were obtained wholly from the literature.
2. The number and form of the elements of the branchiostegal series (operculars, branchiostegals, and gulars) and of the hyoid arch (interhyal, epihyal, ceratohyal, and hypohyals) were studied, defined, described, and depicted. A standard method of enumerating branchiostegals is suggested.
3. The phylogenetic implications of these character complexes were tested against a number of other sound taxonomic characters. Where the changes suggested by the two complexes were supported by other characters, changes in the classification of the teleostomes were made. In other cases, the existing classification or previous classifications were reinforced, or the complexes were at variance with most other characters. The present study incorporates recent changes in classification and may provide a useful summary of current knowledge.
4. The branchiostegal series and hyoid arch were found to offer numerous characters of systematic significance. Forms with a high number of branchiostegals were generally found to be primitive (exceptions are indicated). Usually it is the anteriormost branchiostegals that are lost. Forms with gill membranes separate were found to be more primitive than those with gill membranes united and free from the isthmus or those with gill membranes joined to the isthmus. Primitive teleostomes have only a single hypohyal; advanced ones have two (but some advanced ones lose one or both). The presence of median and lateral gulars or of gular folds is primitive. The interoperculum and apparently the epihyal are absent in primitive teleostomes.
5. The two character complexes offer support for division of the Teleostomi into four subclasses: Actinopterygii, Crossopterygii, Dipneusti, and Brachiopterygii (although the last is not as distinct as the others). But they also give evidence of a common origin of the teleostomes and evidence for placement within a single class (*see* p. 11).
6. The two character complexes and other osteological features support the retention of the three major supraordinal groups—Chondrostei, Holostei, and Teleostei—although with some modification of the included orders

and with some modification of their definition (*see* p. 18–20). The thus reconstituted and redefined groups are believed to be natural (except that some groups are too poorly known for certain placement). The Teleostei themselves are divided into two groups: the Malacopterygii (*see* p. 33) and the Acanthopterygii (*see* p. 89). The constitution and characterization of the latter two groups have been considerably changed (*see* Table 2).

7. The following are some of the suggested changes. Other minor changes will be found at appropriate places in the text:
   - (a) The Mormyriformes show several fundamental similarities to the Osteoglossoidei (including Pantodontoidei) and to the Notopteroidei (excluding Hiodontidae). It is concluded that the last two groups may be accommodated in the order Mormyriformes (*see* p. 62).
   - (b) The Mormyriformes share with the Leptolepiformes similar parasphenoids and hypohyals and differ in these features with the Clupeiformes. It is suggested that the Mormyriformes may have been derived from the Leptolepiformes or their close ancestors and that they may well require removal to the Holostei (*see* p. 63).
   - (c) The Elopoidei, Albuloidei, and Clupeoidei are morphologically distinct and require subordinal separation from one another (*see* p. 35). There may be more than one species of *Albula* (*see* p. 37).
   - (d) The Tselfatoidei belong amongst the primitive Clupeiformes rather than amongst the exocoetoids (*see* p. 43).
   - (e) The Hiodontidae are not closely related to the Notopteridae and require placement in a new suborder Hiodontoidei in the Clupeiformes (*see* p. 44).
   - (f) The Chanoidei (Kneriidae, Chanidae, Phractolaemidae, and Cromeriidae) were found to be characterized by the absence of an ossified interhyal and are thus separable from the Gonorhynchoidei which possess a well-developed interhyal. Other characters support this separation (*see* p. 45).
   - (g) The branchiostegals and several other characters, but not the caudal skeleton, indicate the Esocidae to be more primitive than the Umbridae and Dalliidae (*see* p. 57).
   - (h) The Cretaceous genus *Enchelurus*, previously referred to the Halosauridae, may belong amongst the primitive Anguilliformes (*see* p. 80).
   - (i) The Myctophidae and Neoscopelidae are differentiated from all other Myctophiformes by the possession of only 2 epihyal branchiostegals, a gas bladder, and photophores (*see* p. 90).
   - (j) A number of orders, previously placed amongst the Malacopterygii, are placed amongst the Acanthopterygii: Myctophiformes, Cetomimiformes, Mirapinniformes, and Ateleoptiformes (*see* p. 89, 97, 99, 118).
   - (k) The *beryciform foramen*, a large oval perforation in the centre of

the ceratohyal, is found to be characteristic of several primitive acanthopterygian orders (*see* p. 6).

The *percopsid projection*, an angulation of the anterior base of the fourth branchiostegal, is found in the Ophidiiformes, Gadiformes, and Percopsiformes (*see* p. 6).

The *clupeoid projection*, a bulge broadening the anterior base of the branchiostegals, is found in the clupeoids and in some of their derivatives (*see* p. 6).

(l) The ophidioids require removal from the Perciformes and association with the Gadiformes and Ateleopiformes in a new order, Ophidiiformes (*see* p. 114).

(m) The Amblyopsidae are included in the Percopsiformes (*see* p. 123).

(n) The Anabantoidei, the Luciocephaloidei, and the Ophicephaloidei are closely related acanthopterygians well-distinguished from the Perciformes, and they require placement in the same order, Ophicephaliformes (*see* p. 133).

(o) The orders Bathyclupeiformes, Polynemiformes, Mugiliformes (in part), Coryphaeniformes, Thunniformes, and Dactylopteriformes are considered synonymous of the order Perciformes.

8. The general relationships of the orders may be seen in the endpapers and in Figs. 2 and 3. Table 1 provides a summary of the differences in the studied structures in the various orders. Table 2 summarizes the classifications of Regan, Berg, Bertin and Arambourg, and of the present study (the present study embodies suggested changes by recent authors). Plates at the end of the text depict variation in the studied structures.

Addenda

Note 1. A new Crossopterygian order, Struniiformes, including a single family Onychodontidae, has been named. The branchiostegal series would suggest placement in the superorder Osteolepides. In the Berg ordinal system the order is based on the name of one of the included families; Struniiformes should therefore be replaced by a name based on Onychodontidae. *See* Hans Jessen. 1967. Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtigung von amerikanischem und europäischem. *Onychodus*—Material. Arkiv för Zoologi 18 (¾): 305–391, 15 text-fig., 22 pl.

Note 2. The Macristiidae has been placed in a new suborder Macristioidei, with a new genus having 16 branchiostegals, 5 of which are on the epihyal. This combination supports clupeiform placement. *See* F. H. Berry and C. R. Robins. 1967. *Macristiella perlucens*, a new clupeiform fish from the Gulf of Mexico. Copeia (1): 46–50, 4 fig.

Note 3. *Material examined.* None. *References*: Chapman (1942), Cohen (1957).

Note 4. The new Eocene family, Beerichthyidae, may be tentatively placed in the Saccopharyngiformes, although it may be related to the Myctophiformes or Cetomimiformes. The operculum is somewhat anguilliform in character. *See* E. Casier. 1966. Faune ichthyologique du London Clay. British Mus., London 407 p. + atlas.

Note 5. *See* R. Haedrich. 1967. The stromateoid fishes: systematics and a classification. Bull. Mus. Comp. Zool. 135: 31–139, 56 fig.

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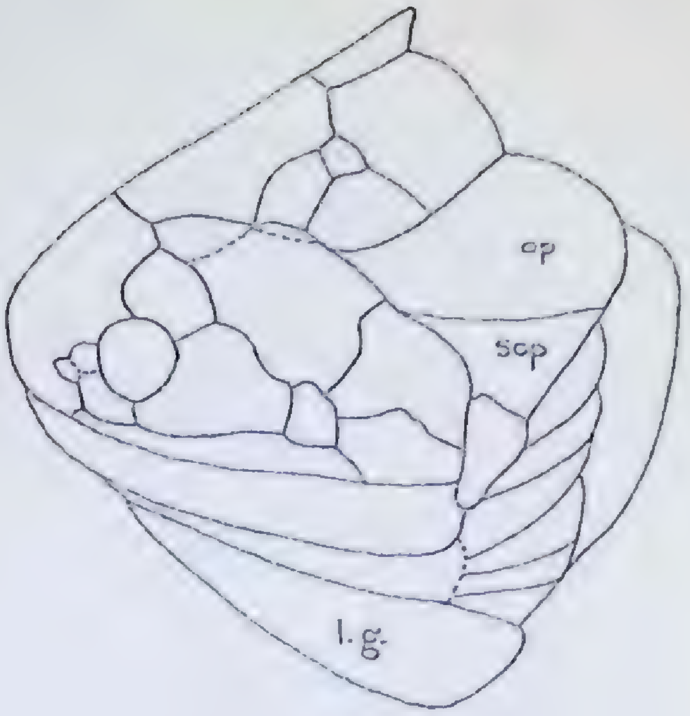
PLATES

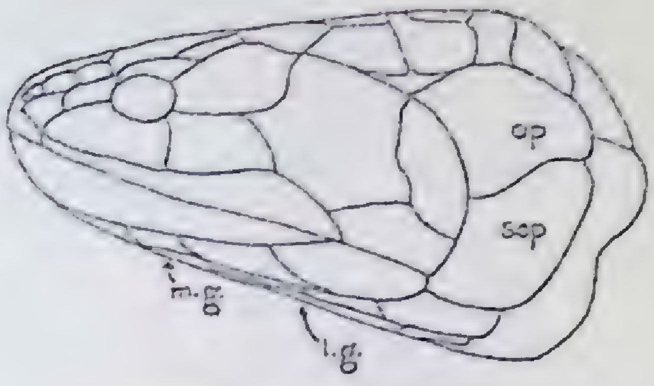
ABBREVIATIONS

a.l.g. = anterior lateral gular
br = branchiostegal
ch = ceratohyal
eh = epihyal
hh = hypohyal
ih = interhyal
iop = interoperculum
l.g. = lateral gular
m.g. = median gular
op = operculum
p.l.g. = posterior lateral gular
sop = suboperculum
sy = symplectic

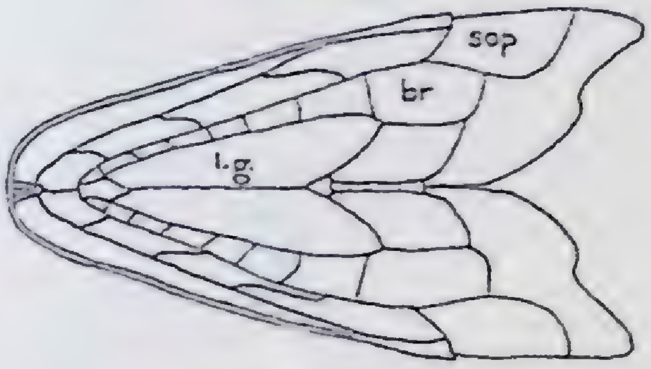
PLATE ONE

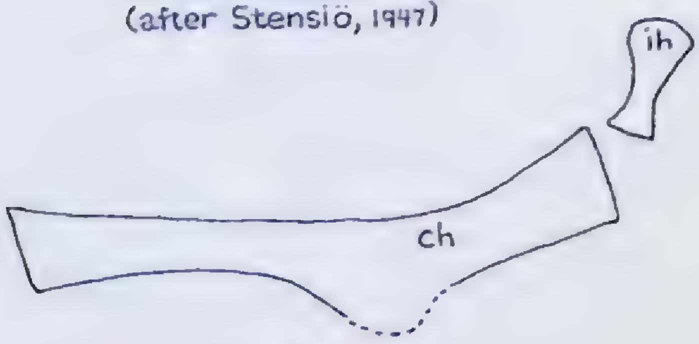


Holoptychius flemingi
POROLEPIFORMES
(after Stensiö, 1947)

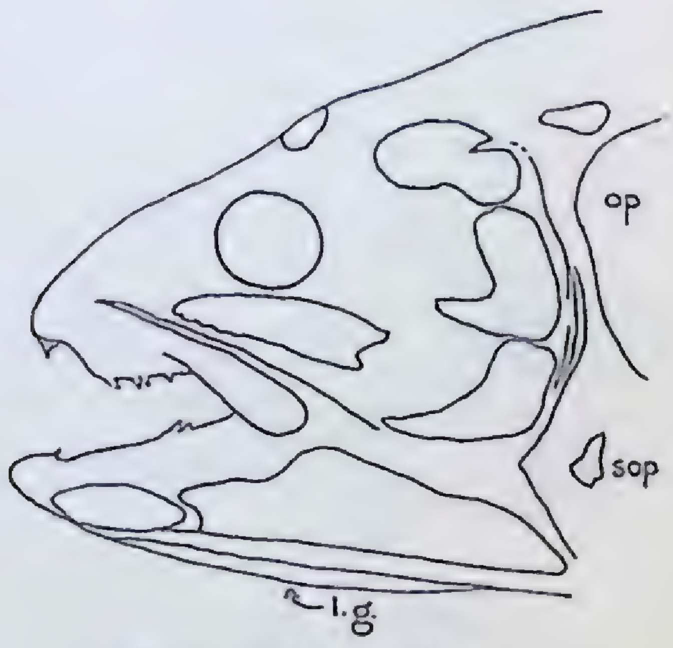


Eusthenopteron foordi
OSTEOLEPIFORMES
(after Jarvik, 1963)

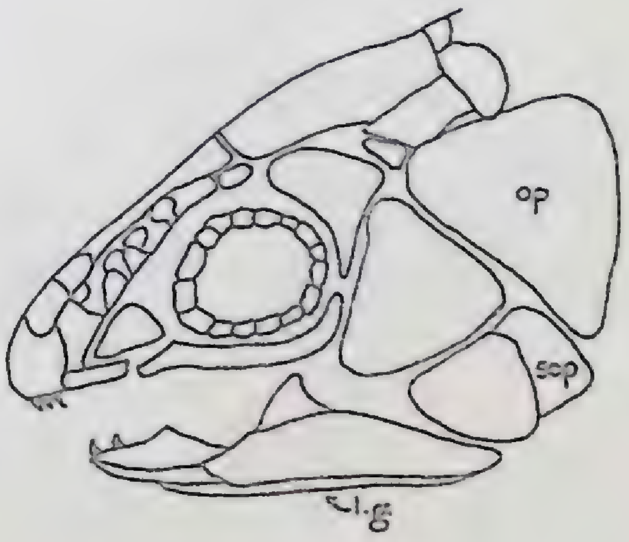




Wimania sinuosa
COELACANTHIFORMES
(after Stensiö, 1921)



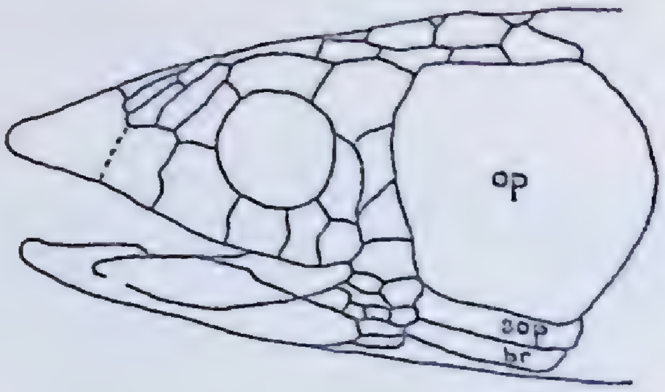
Latimeria chalumnae
COELACANTHIFORMES
(after Stensiö, 1947)



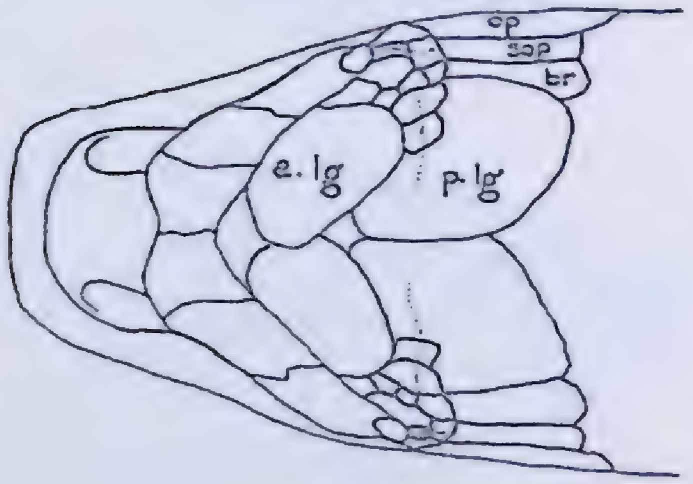
Rhabdoderma elegans
COELACANTHIFORMES
(after Berg, 1955)

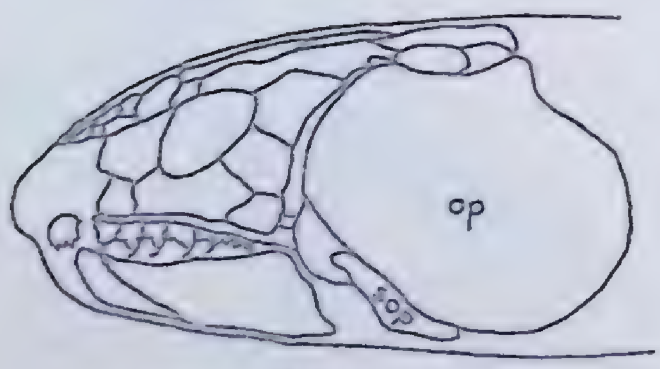
Branchiostegal series and hyoid arch in Crossopterygii.

PLATE TWO

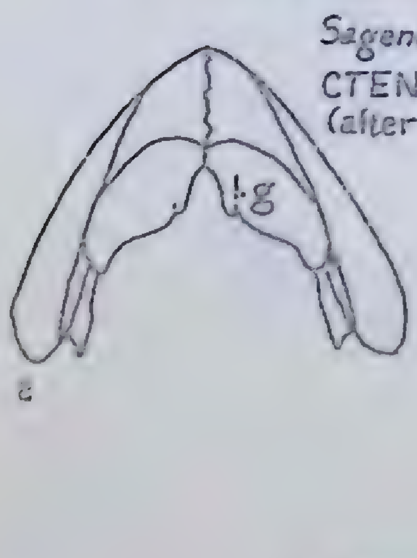


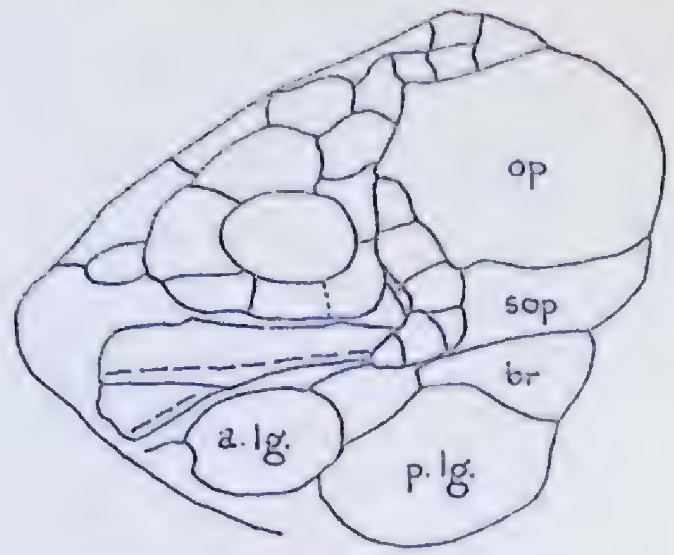
Dipterus valenciennesi
DIPTERIFORMES
(after Stensiö, 1947)



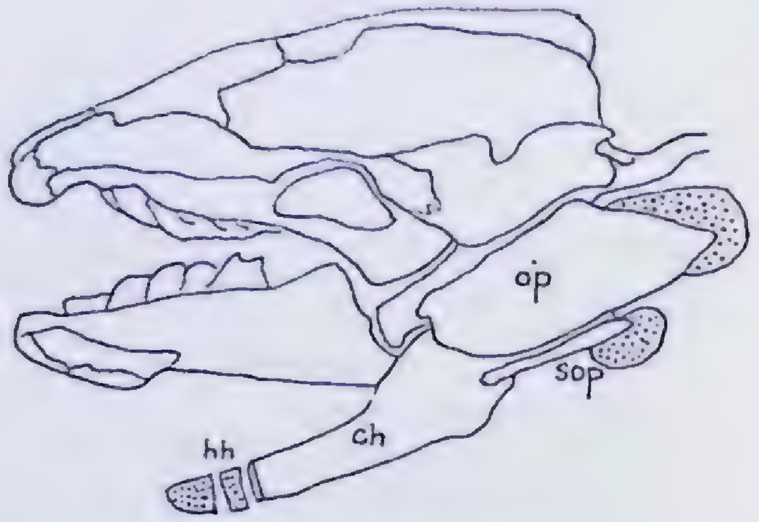


Sagenodus
CTENODONTIFORMES
(after Watson & Gill, 1923)

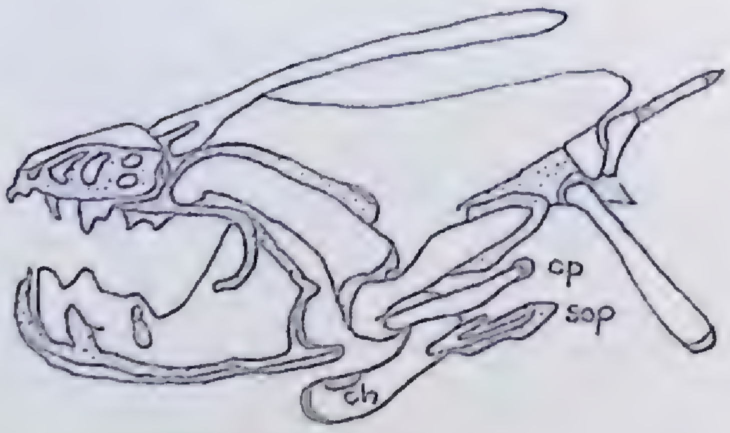




Scaumenacia curta
PHANEROPLEURIFORMES
(after Stensiö, 1947)



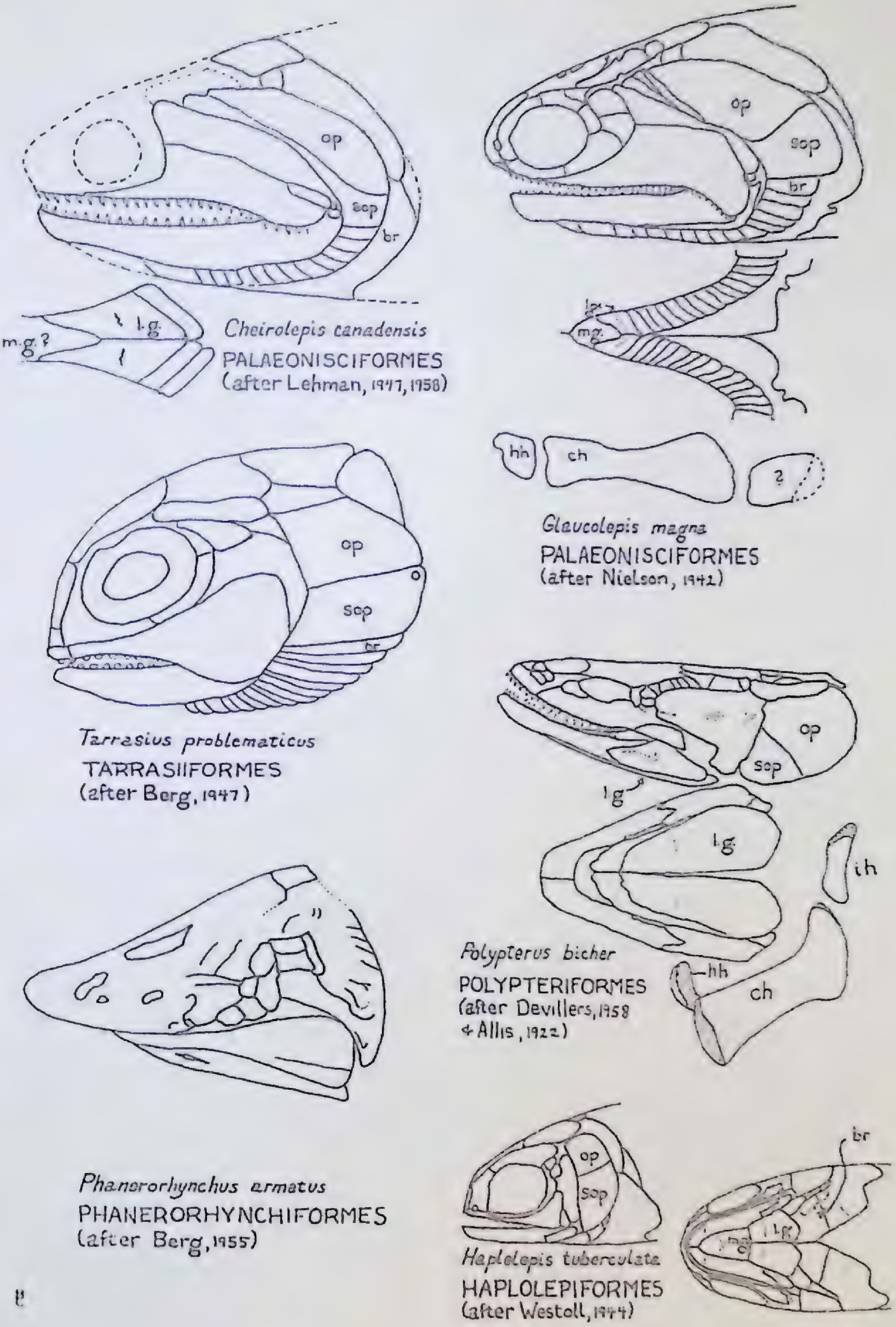
Neoceratodus forsteri
CERATODIDIFORMES



Lepidosiren paradoxa
LEPIDOSIRENIFORMES
(after Bridge, 1898)

Branchiostegal series and hyoid arch in Dipneusti.

PLATE THREE



Cheirolepis canadensis
PALAEONISCIFORMES
(after Lehman, 1947, 1958)

Glaucolepis magna
PALAEONISCIFORMES
(after Nielson, 1942)

Tarrasius problematicus
TARRASIIFORMES
(after Berg, 1947)

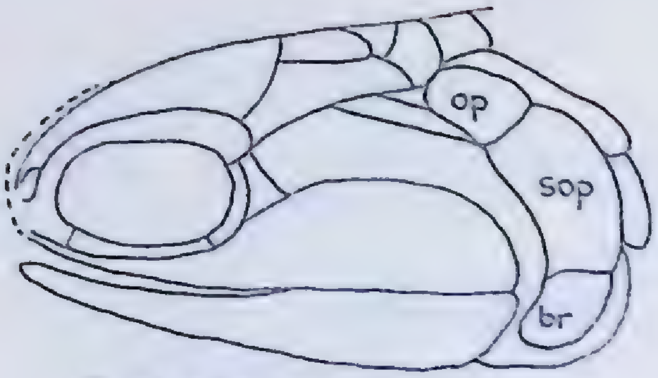
Polypterus bicher
POLYPTERIFORMES
(after Devillers, 1958
& Allis, 1922)

Phanerorhynchus armatus
PHANERORHYNCHIFORMES
(after Berg, 1955)

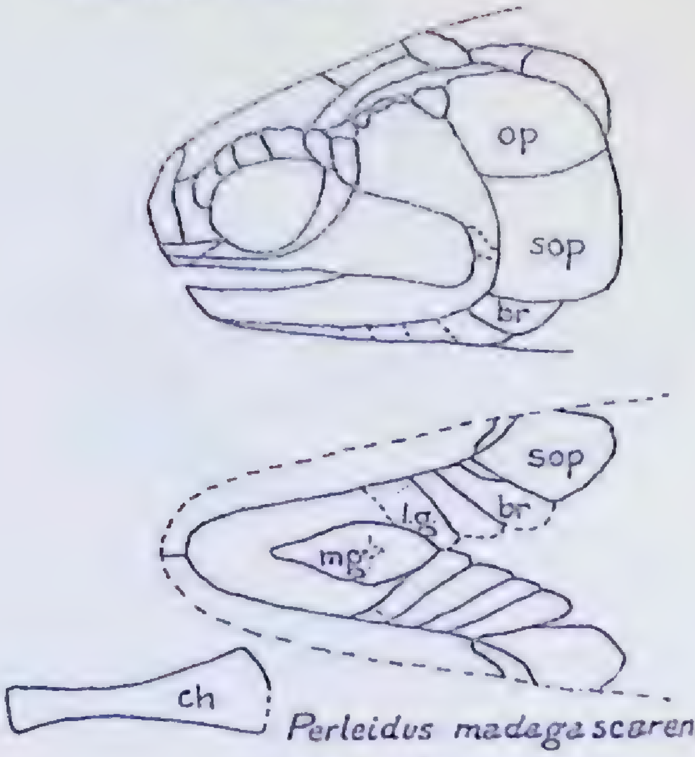
Haplolepis tuberculata
HAPLOLEPIFORMES
(after Westoll, 1944)

Branchiostegal series and hyoid arch in Chondrostei and Brachiopterygii.

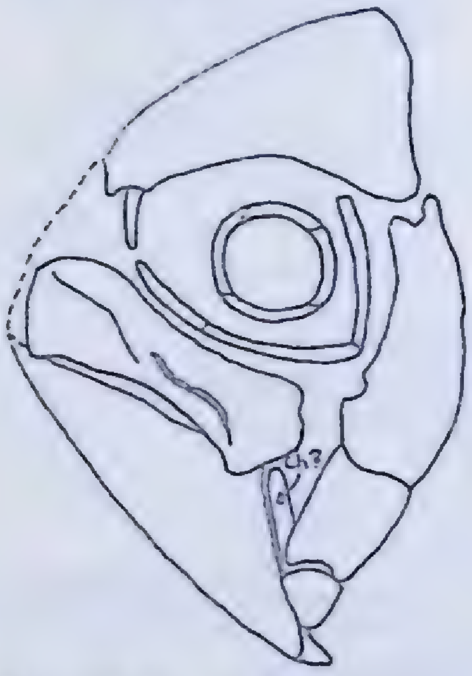
PLATE FOUR



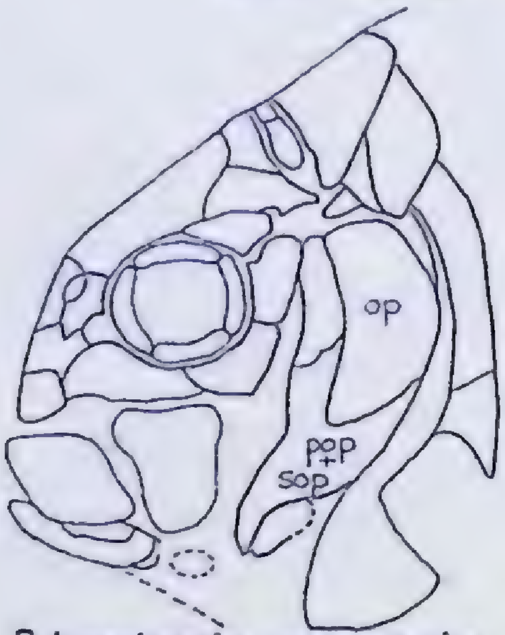
Brookvalia gracilis
REDFIELDIIFORMES
(after Berg, 1955)



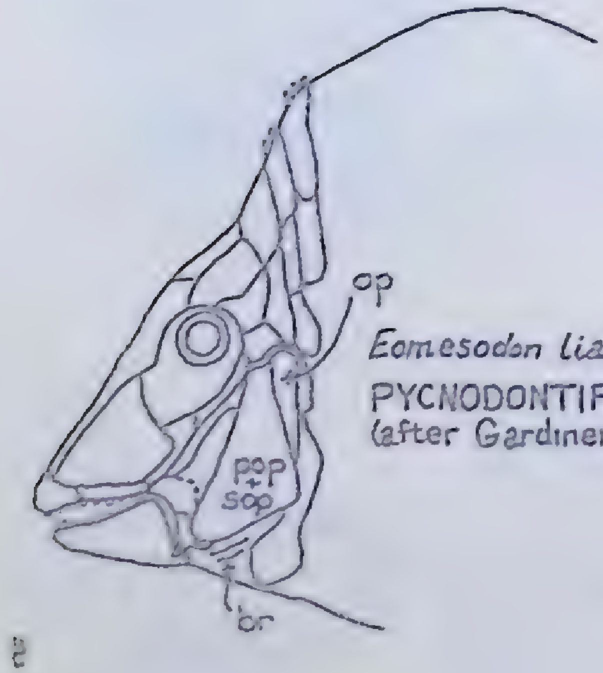
Perleidus madagascarensis
PERLEIDIFORMES
(after Lehman, 1952)



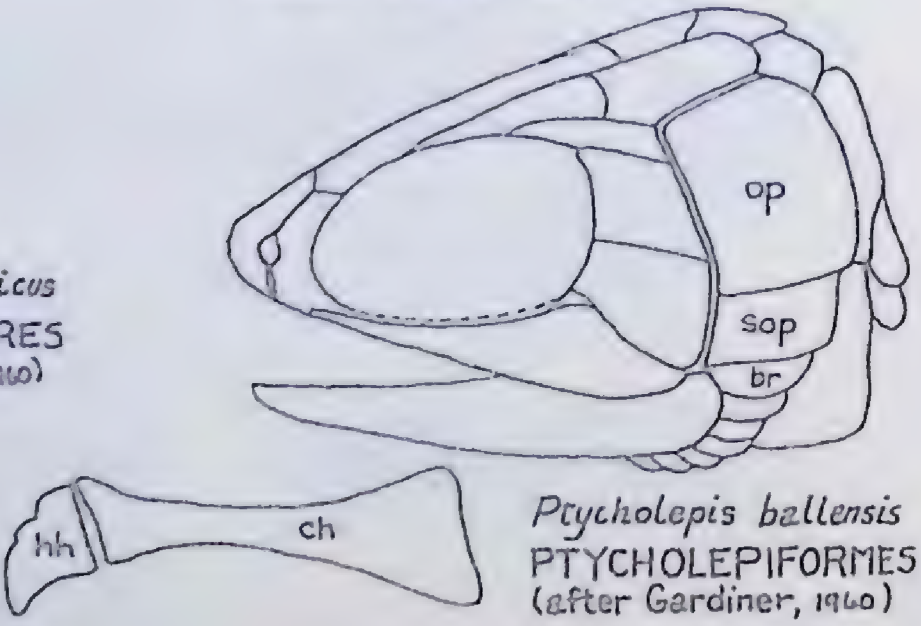
Dorypterus hoffmanni
DORYPTERIFORMES
(after Westoll, 1941)



Bobasatrania mahavavica
BOBASATRANIIFORMES
(after Lehman, 1953)



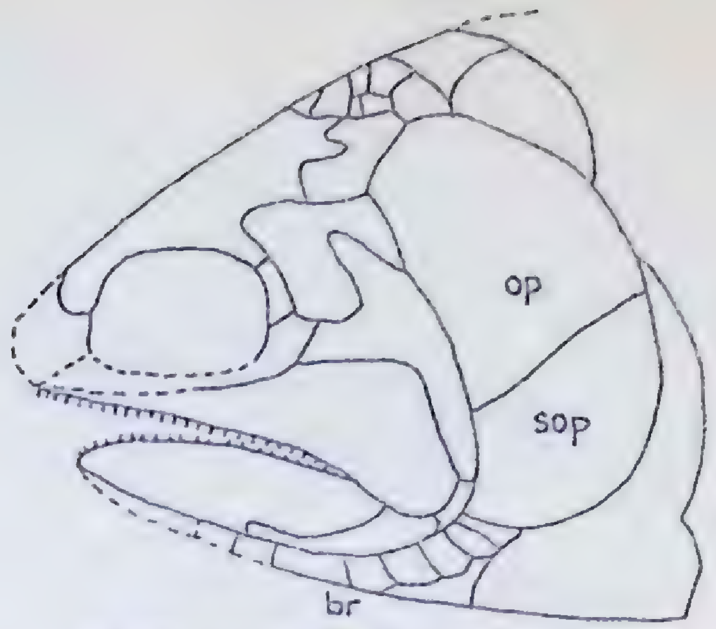
Eomesodon liassicus
PYCNODONTIFORES
(after Gardiner, 1960)



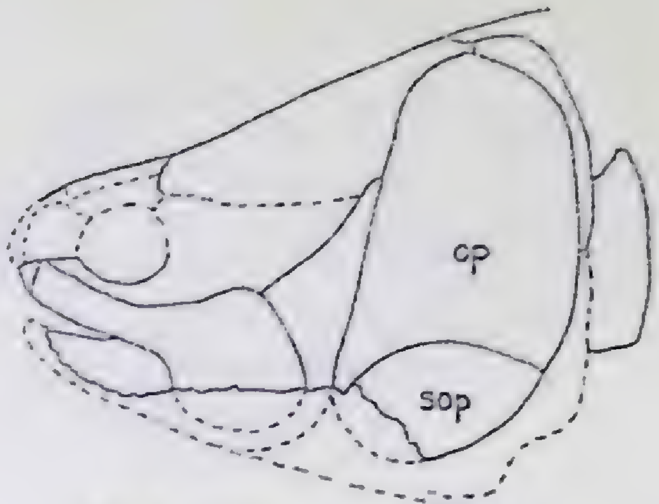
Ptycholepis bollensis
PTYCHOLEPIFORMES
(after Gardiner, 1960)

Branchiostegal series and hyoid arch in Chondrostei (*cont.*).

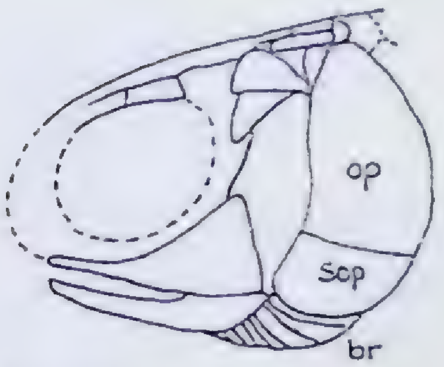
PLATE FIVE



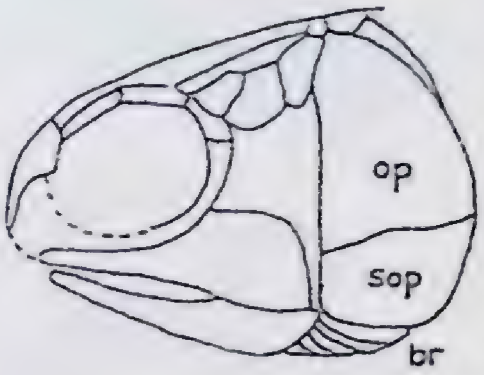
Australosumus merlei
PHOLIDOPLEURIFORMES
(after Lehman, 1952)



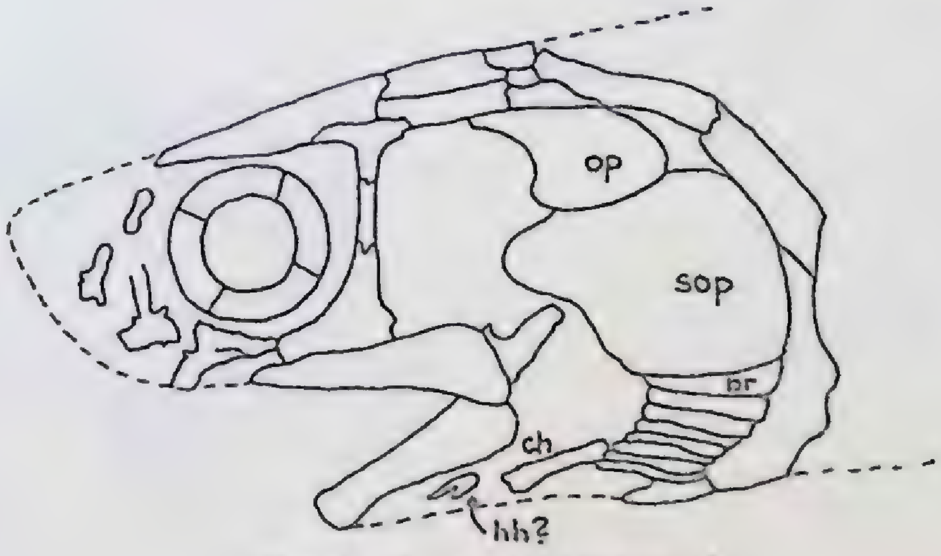
Cephaloxenus macropterus
CEPHALOXENIFORMES
(after Brough, 1939)



Peltopleurus rugosus
PELTOPLEURIFORMES
(after Brough, 1939)



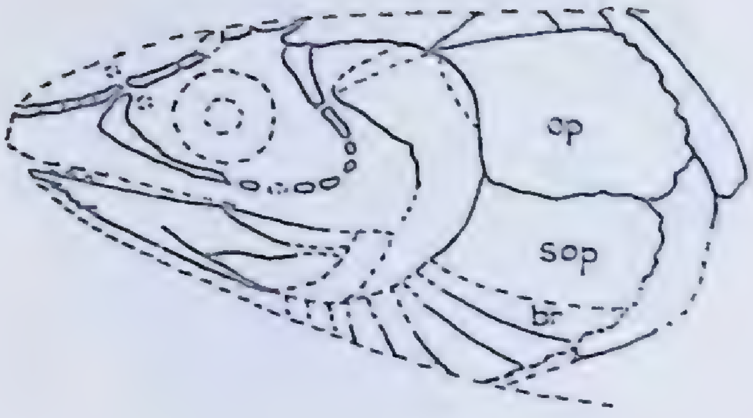
Peltopleurus lissocephalus
PELTOPLEURIFORMES
(after Brough 1939)



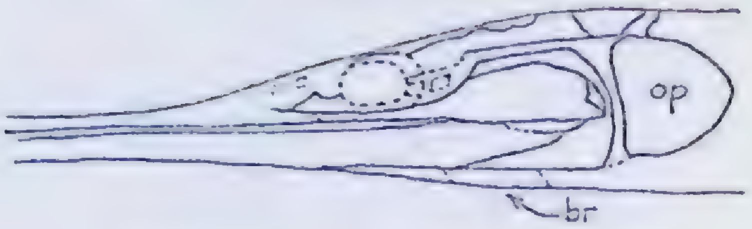
Chondrosteus acipenseroides
CHONDROSTEIFORMES
(after Lehman, 1958)

Branchiostegal series and hyoid arch in Chondrostei (*cont.*).

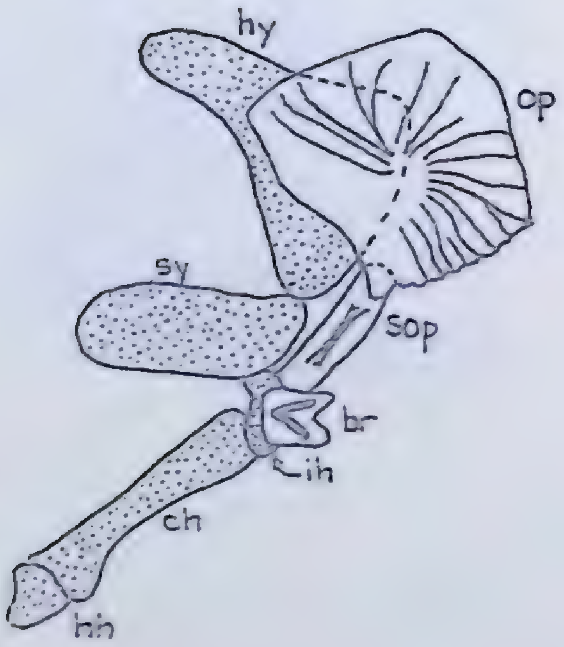
PLATE SIX



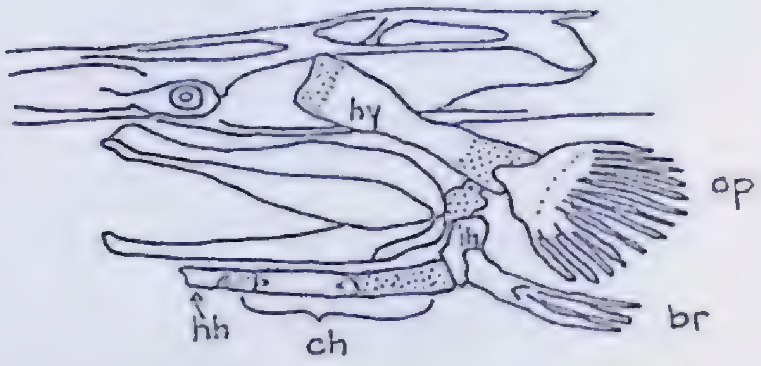
Errolichthys mirabilis
CHONDROSTEIFORMES
(after Lehman, 1952)



Saurichthys madagascarensis
SAURICHTHYIFORMES
(after Lehman, 1952)

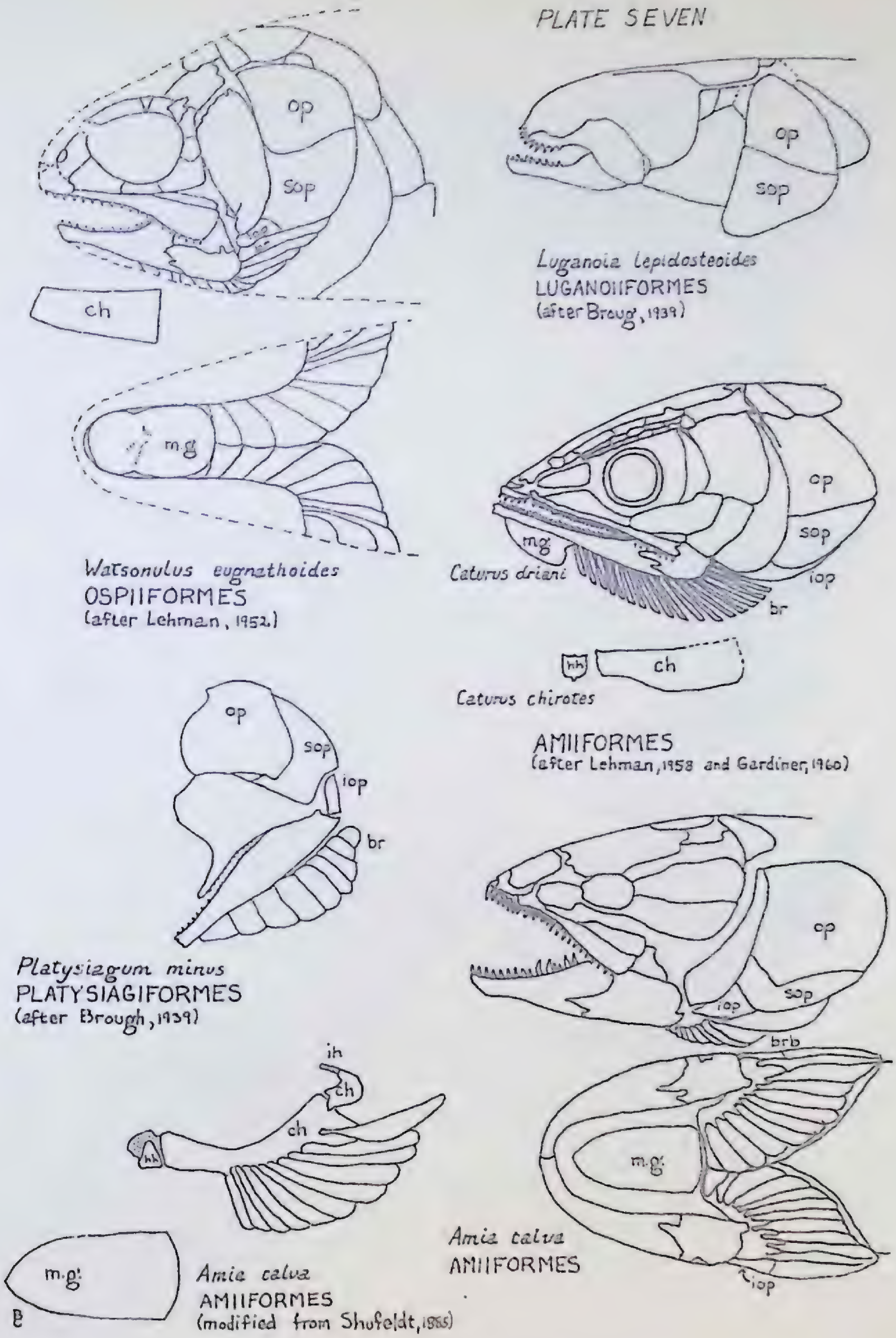


Acipenser fulvesens
ACIPENSERIFORMES



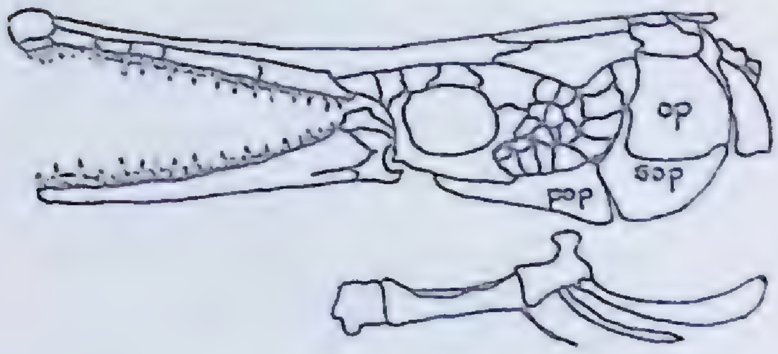
Polyodon spathula
ACIPENSERIFORMES
(modified after Bertin, 1958)

Branchiostegal series and hyoid arch in Chondrostei (*cont.*).

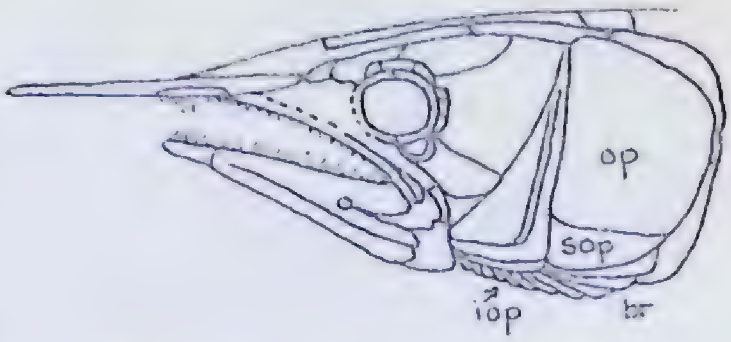


Branchiostegal series and hyoid arch in Holostei.

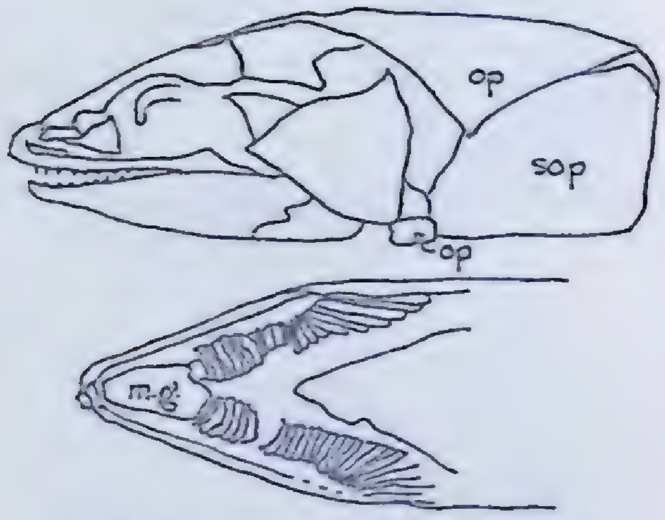
PLATE EIGHT



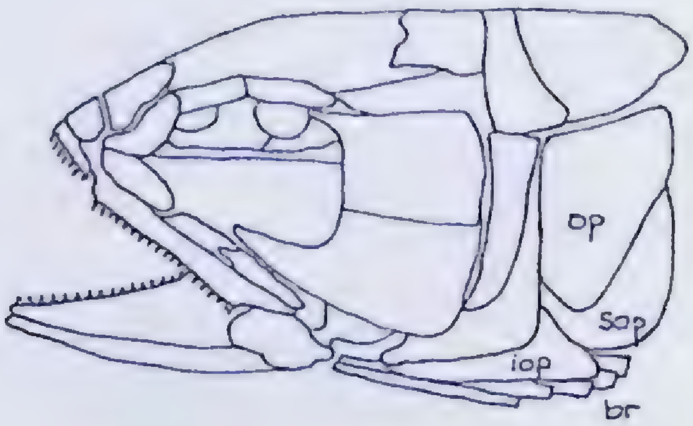
Lepisosteus
LEPISOSTEIFORMES



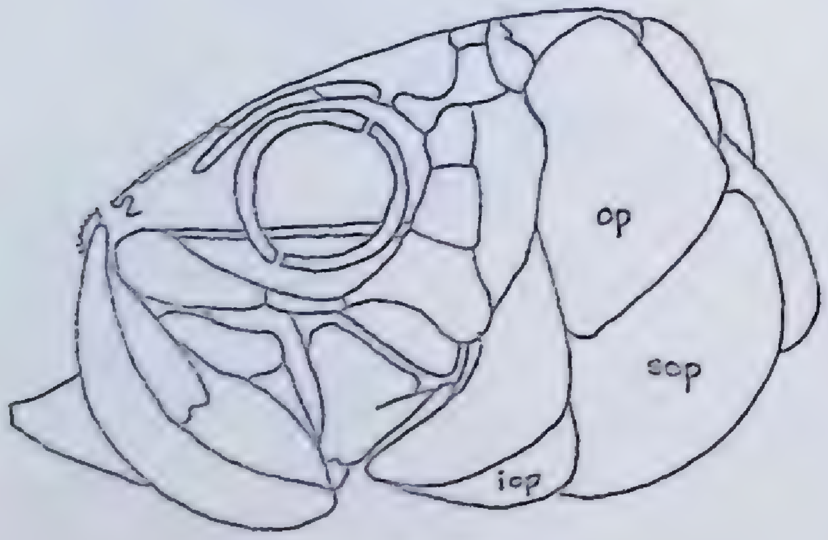
Aspidorhynchus acutirostris
ASPIDORHYNCHIFORMES
(after Berg, 1955)



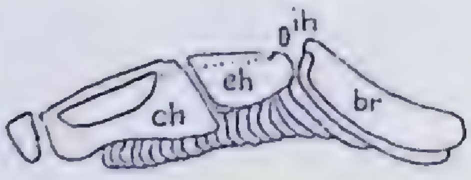
Pachycormus macropterus
PACHYCORMIFORMES
(after Zittel, 1887)



Pholidophorus similis
PHOLIDOPHORIFORMES
(after Bertin + Arambourg, 1958)



Leptolepis bronni

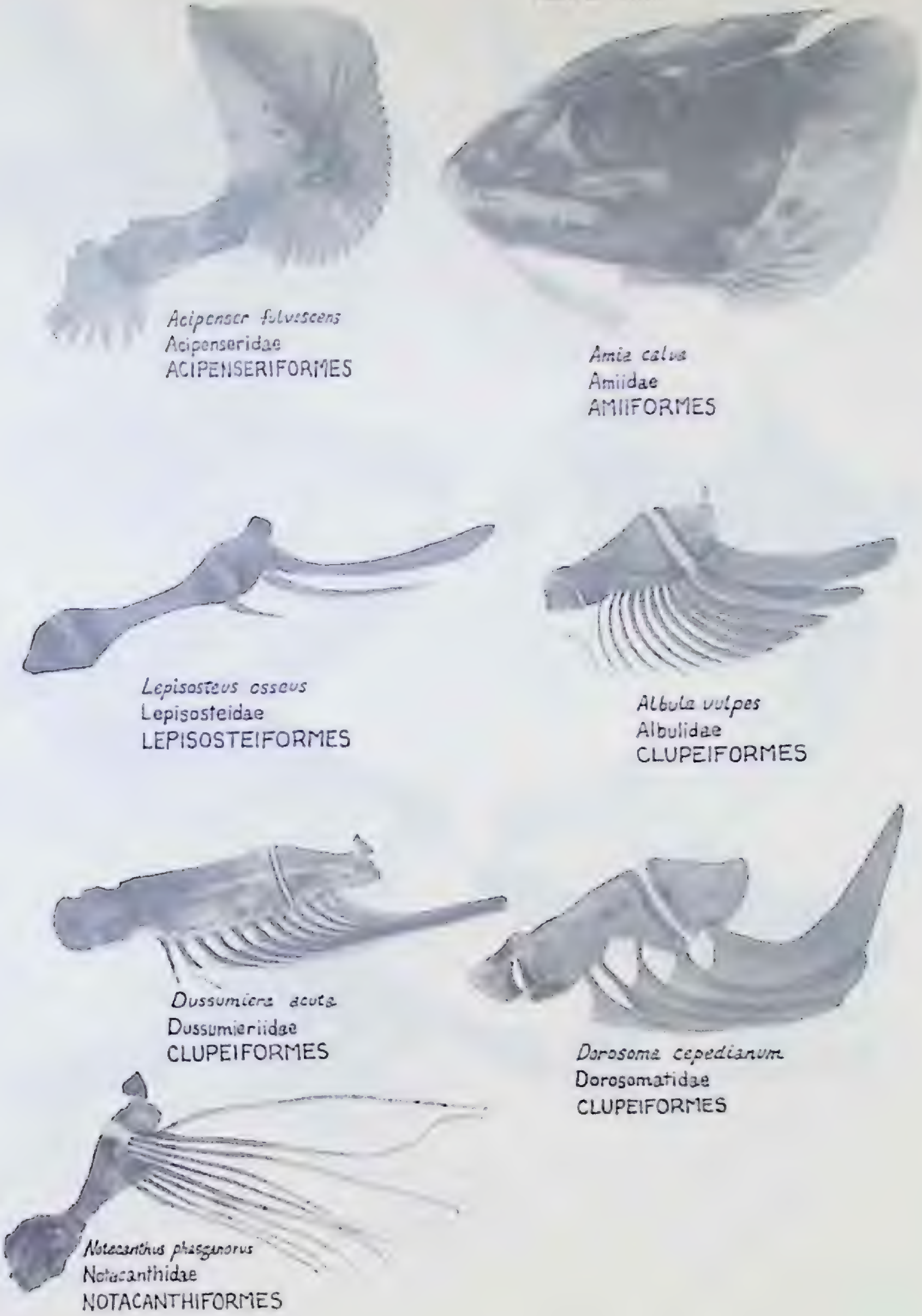


Leptolepis dubius

LEPTOLEPIFORMES
(after Berg, 1955, Woodward, 1895,)
Rayner, 1937

Branchiostegal series and hyoid arch in Holostei (*cont.*).

PLATE NINE



Acipenser fulvescens
Acipenseridae
ACIPENSERIFORMES

Amia calva
Amiidae
AMIIFORMES

Lepisosteus osseus
Lepisosteidae
LEPISOSTEIFORMES

Albula vulpes
Albulidae
CLUPEIFORMES

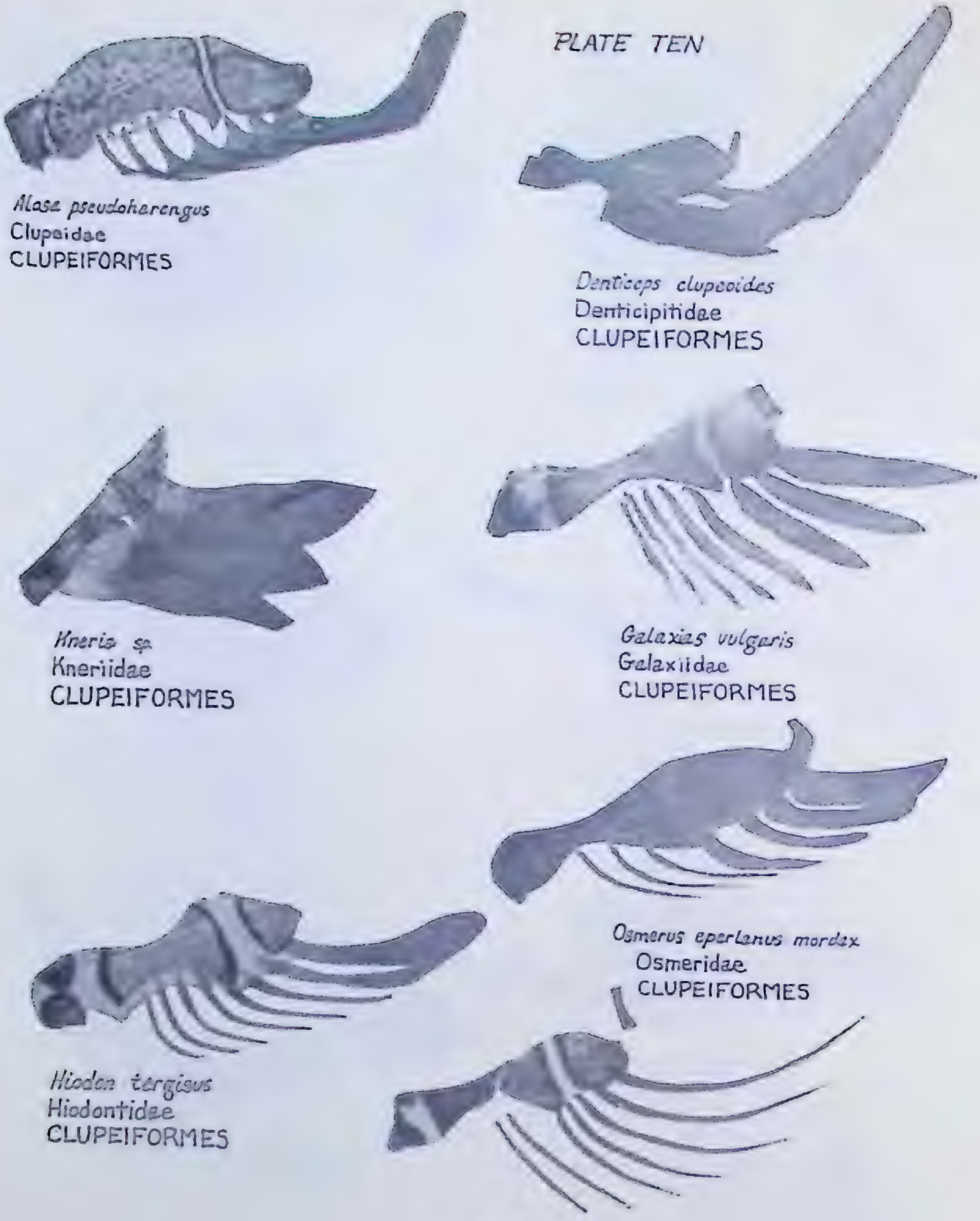
Dussumieria acuta
Dussumieriidae
CLUPEIFORMES

Dorosoma cepedianum
Dorosomatidae
CLUPEIFORMES

Notacanthus phasganorus
Notacanthidae
NOTACANTHIFORMES

Branchiostegal series and hyoid arch in Chondrostei, Holostei, and Teleostei.

PLATE TEN



Alosa pseudoharengus
Clupeidae
CLUPEIFORMES

Denticeps clupeoides
Denticipitidae
CLUPEIFORMES

Kneria sp.
Kneriidae
CLUPEIFORMES

Galaxias vulgaris
Galaxiidae
CLUPEIFORMES

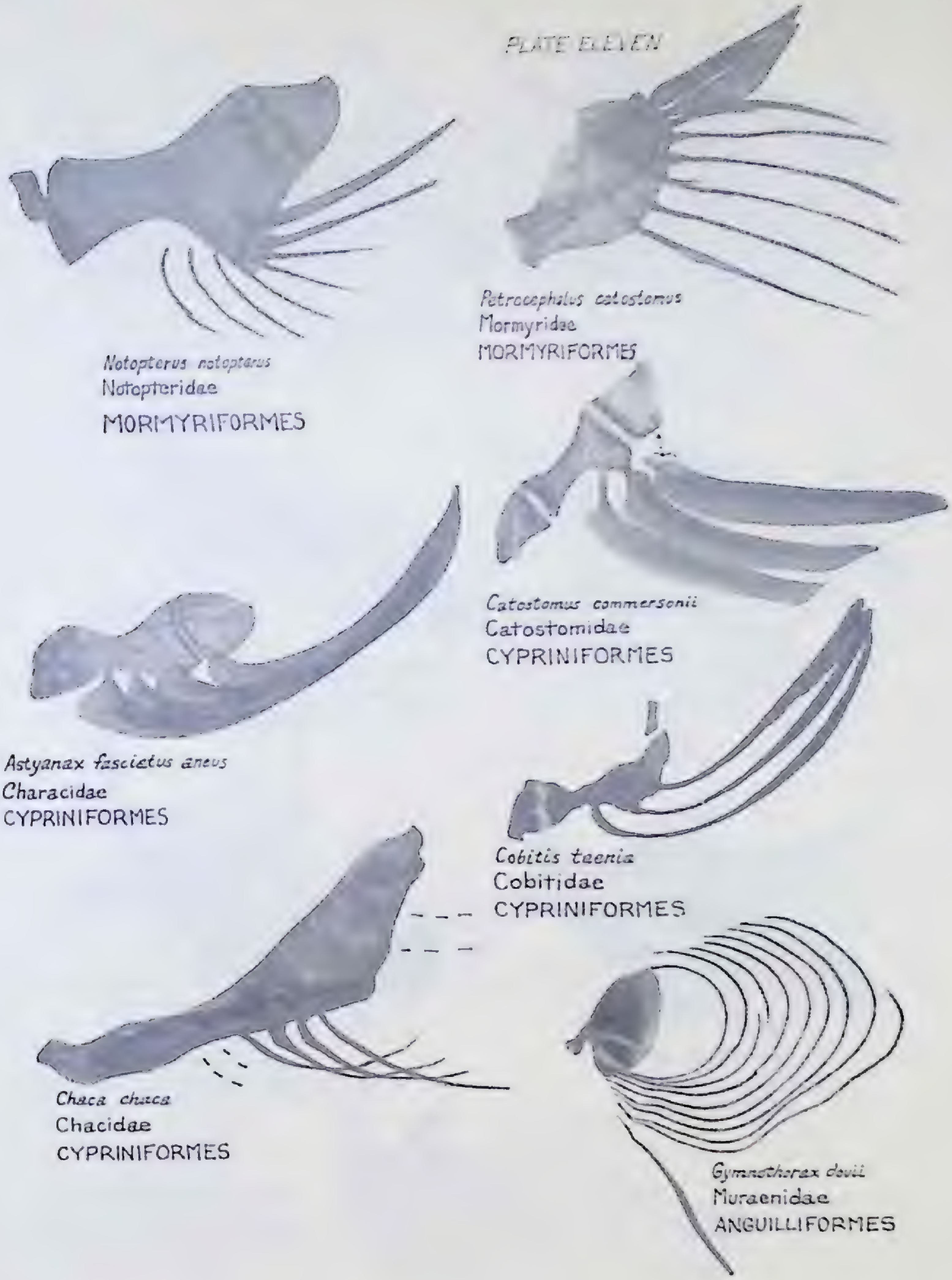
Osmerus eperlanus mordax
Osmeridae
CLUPEIFORMES

Hiodon tergisus
Hiodontidae
CLUPEIFORMES

Dallia pectoralis
Dalliidae
CLUPEIFORMES

Branchiostegal series and hyoid arch in Malacopterygii.

PLATE ELEVEN



Notopterus notopterus
Notopteridae
MORMYRIFORMES

Petrocephalus catostomus
Mormyridae
MORMYRIFORMES

Catostomus commersonii
Catostomidae
CYPRINIFORMES

Astyanax fasciatus aneus
Characidae
CYPRINIFORMES

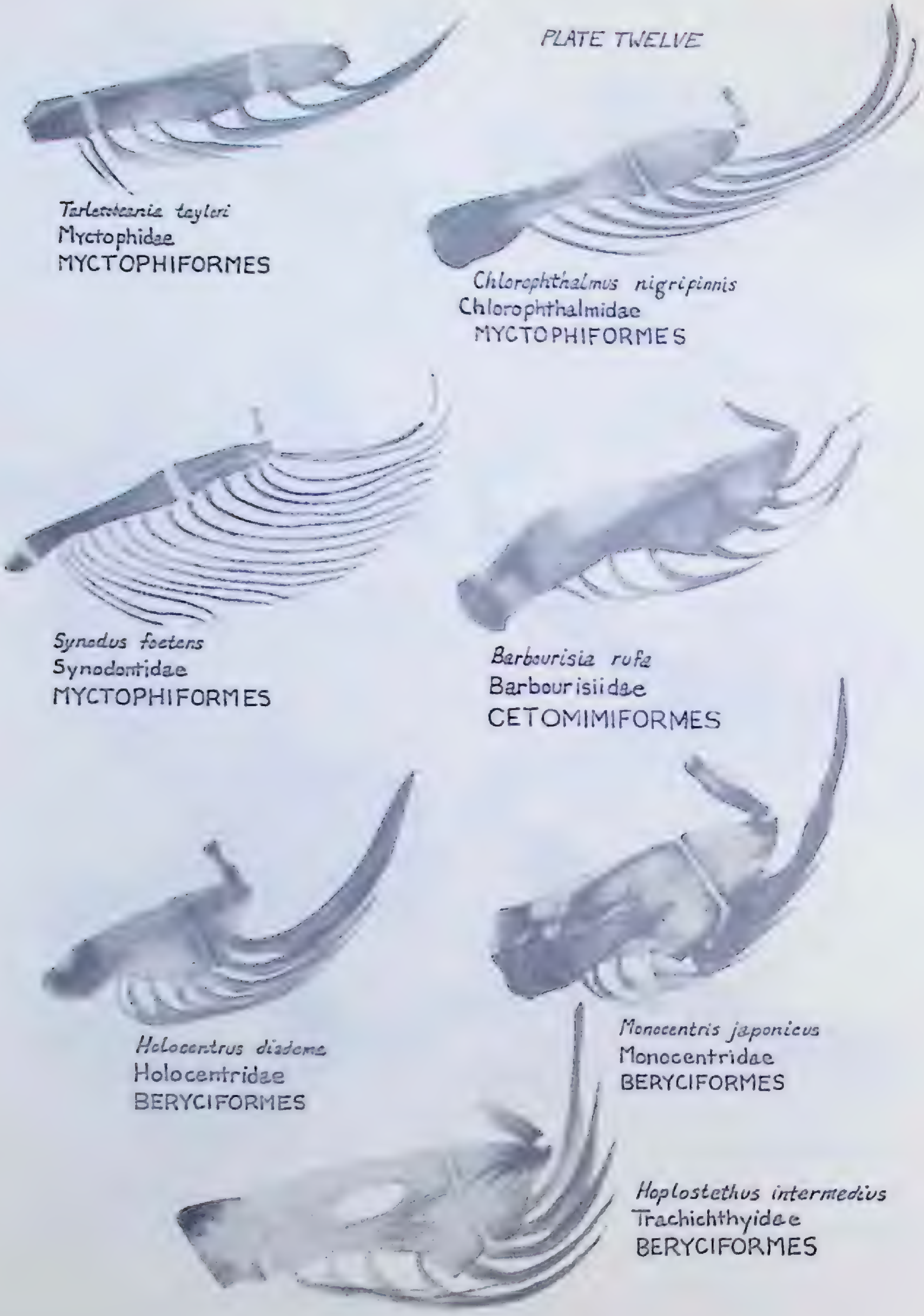
Cobitis taenia
Cobitidae
CYPRINIFORMES

Chaca chaca
Chacidae
CYPRINIFORMES

Gymnothorax dovii
Muraenidae
ANGUILLIFORMES

Branchiostegal series and hyoid arch in Malacopterygii.

PLATE TWELVE



Tarletonbeania tayleri
Myctophidae
MYCTOPHIFORMES

Chlorophthalmus nigripinnis
Chlorophthalmidae
MYCTOPHIFORMES

Synodus foetens
Synodontidae
MYCTOPHIFORMES

Barbourisia rufa
Barbourisiidae
CETOMIMIFORMES

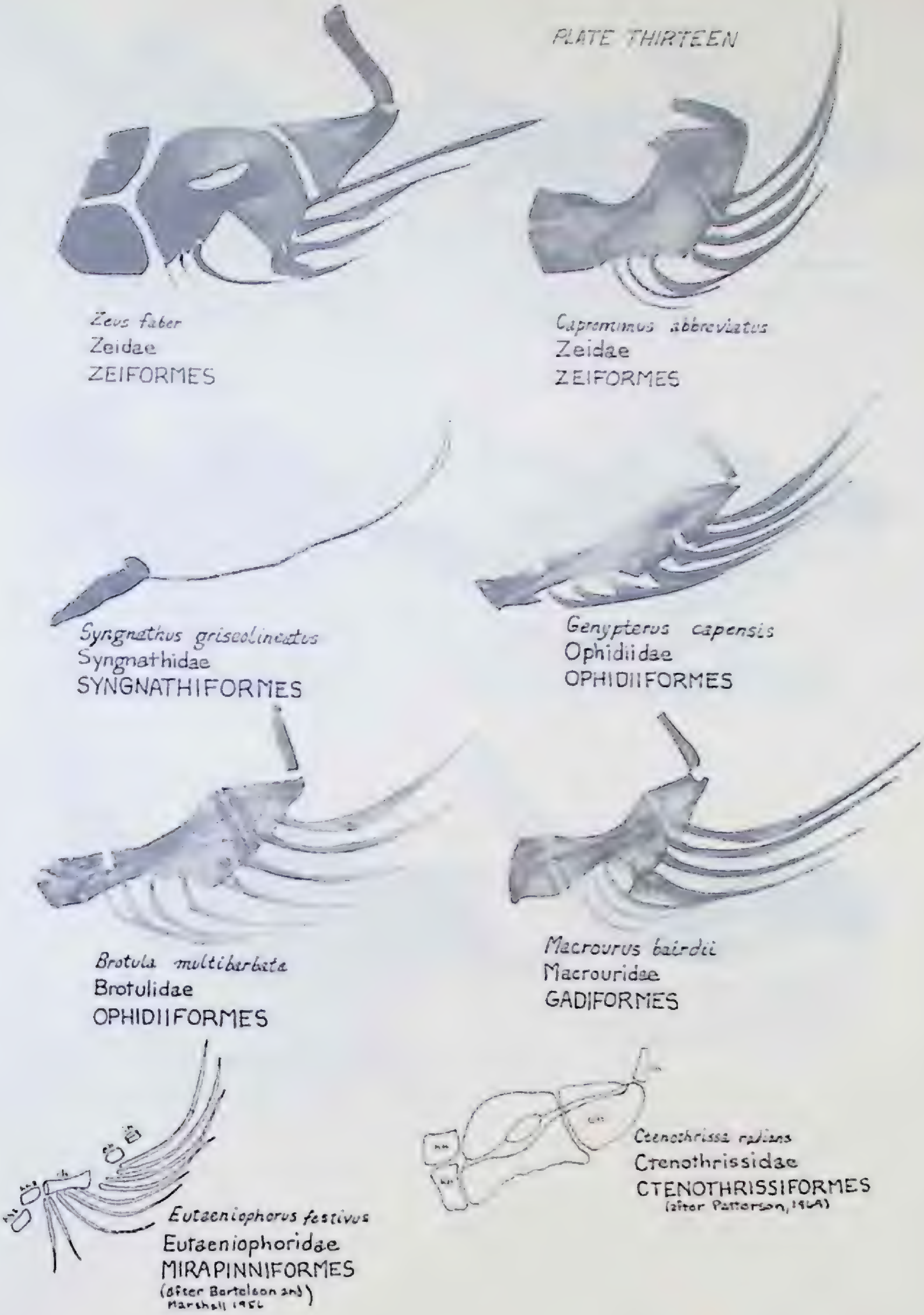
Holocentrus diadema
Holocentridae
BERYCIFORMES

Monocentris japonicus
Monocentridae
BERYCIFORMES

Hoplostethus intermedius
Trachichthyidae
BERYCIFORMES

Branchiostegal series and hyoid arch in Acanthopterygii.

PLATE THIRTEEN



Zeus faber
Zeidae
ZEIFORMES

Capromimus abbreviatus
Zeidae
ZEIFORMES

Syngnathus griseolineatus
Syngnathidae
SYNGNATHIFORMES

Genypterus capensis
Ophidiidae
OPHIDIIFORMES

Brotula multibarbata
Brotulidae
OPHIDIIFORMES

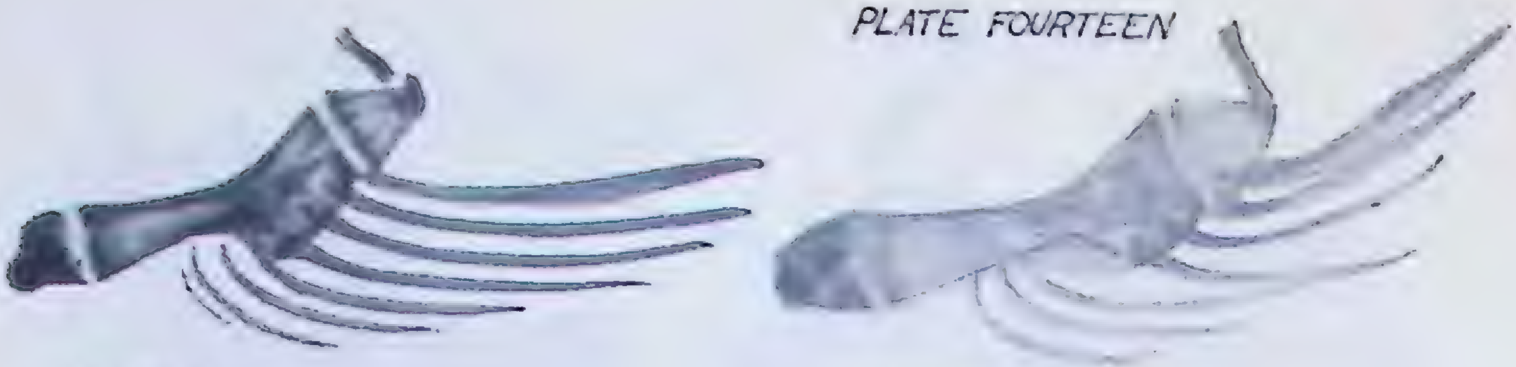
Macrourus bairdii
Macrouridae
GADIFORMES

Eutaeniophorus festivus
Eutaeniophoridae
MIRAPINNIFORMES
(after Bertelson and Marshall 1956)

Ctenothrissa radians
Ctenothrissidae
CTENOTHRISSIFORMES
(after Patterson, 1964)

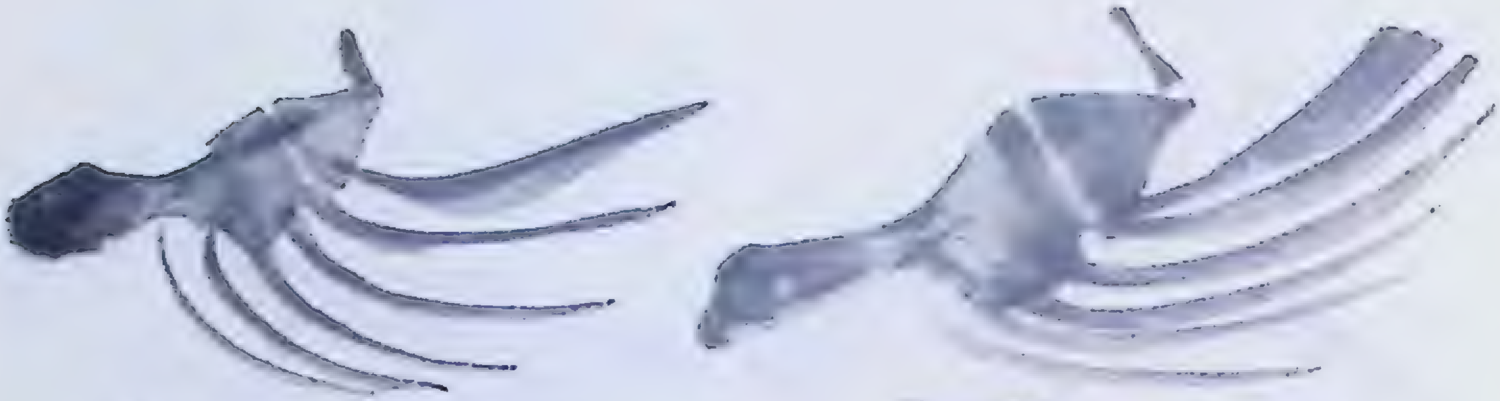
Branchiostegal series and hyoid arch in Acanthopterygii.

PLATE FOURTEEN



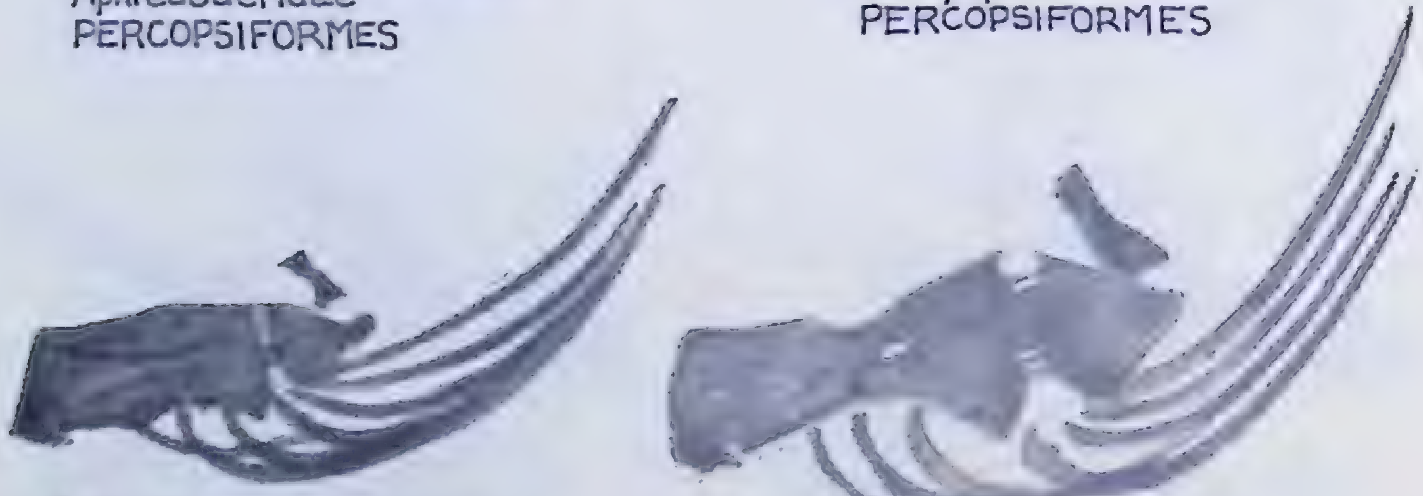
Lota lota
Gadidae
GADIFORMES

Antimora rostrata
Moridae
GADIFORMES



Aphredoderus sayanus gibbosus
Aphredoderidae
PERCOPSIFORMES

Typhlichthys subterraneous
Amblyopsidae
PERCOPSIFORMES

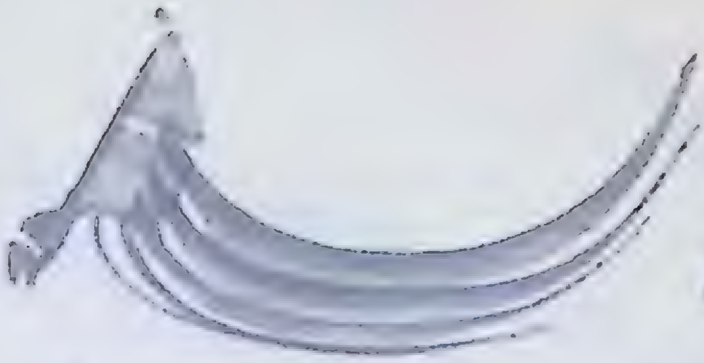


Psettichthys melanostictus
Pleuronectidae
PLEURONECTIFORMES

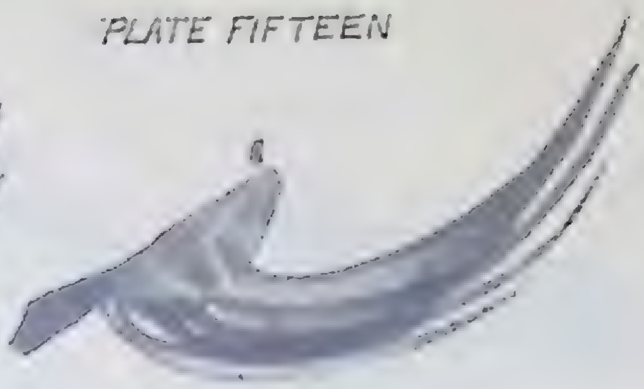
Scopthalmus aquosus
Bothidae
PLEURONECTIFORMES

Branchiostegal series and hyoid arch in Acanthopterygii.

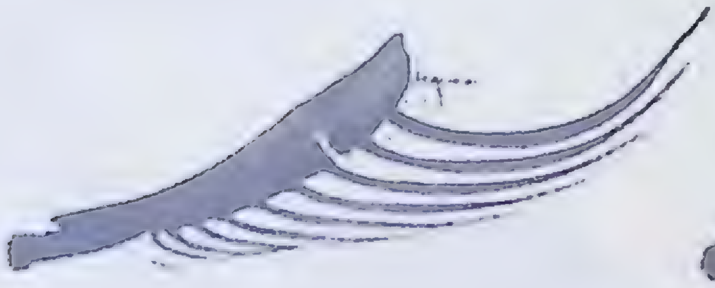
PLATE FIFTEEN



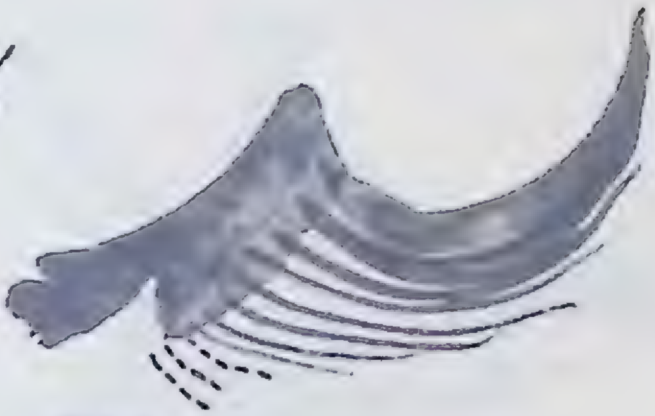
Poeciliopsis viriosa
Poeciliidae
ATHERINIFORMES



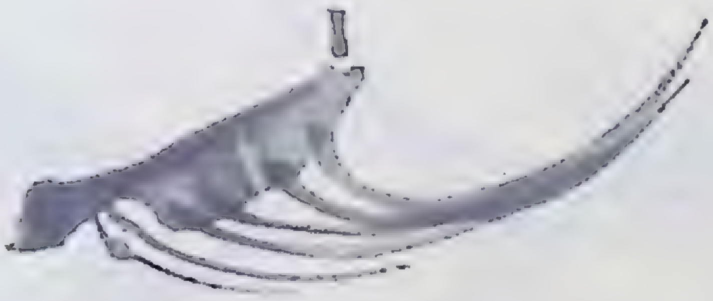
Anableps dovii
Anablepidae
ATHERINIFORMES



Tylosaurus marinus
Belonidae
ATHERINIFORMES



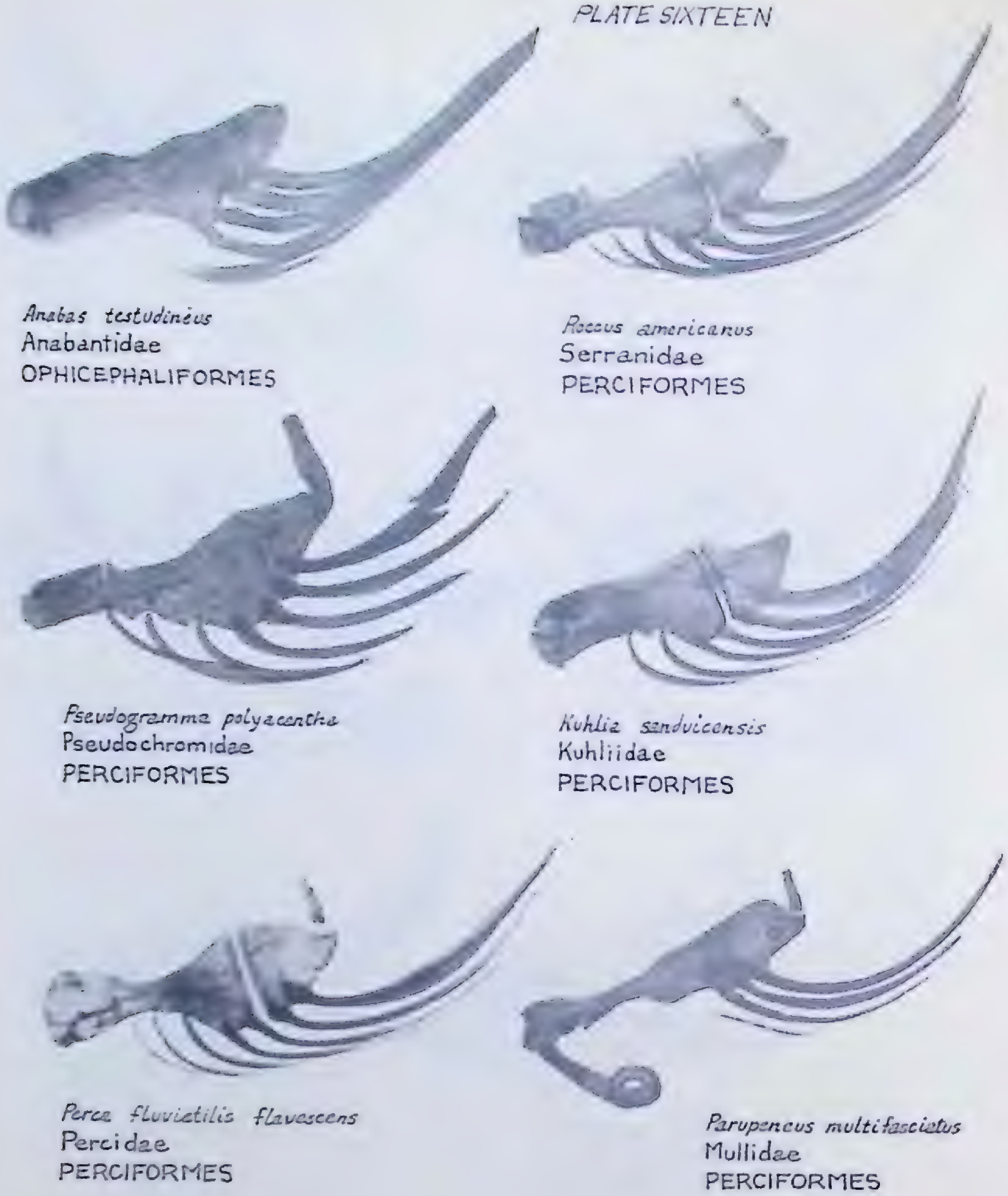
Fodiator acutus
Exocoetidae
ATHERINIFORMES



Menidia menidia
Atherinidae
ATHERINIFORMES

Branchiostegal series and hyoid arch in Acanthopterygii.

PLATE SIXTEEN



Anabas testudineus
Anabantidae
OPHICEPHALIFORMES

Roccus americanus
Serranidae
PERCIFORMES

Pseudogramma polyacantha
Pseudochromidae
PERCIFORMES

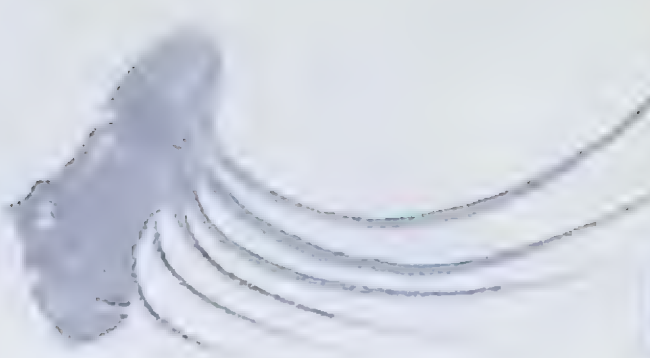
Kuhlia sandvicensis
Kuhliidae
PERCIFORMES

Perca fluviatilis flavescens
Percidae
PERCIFORMES

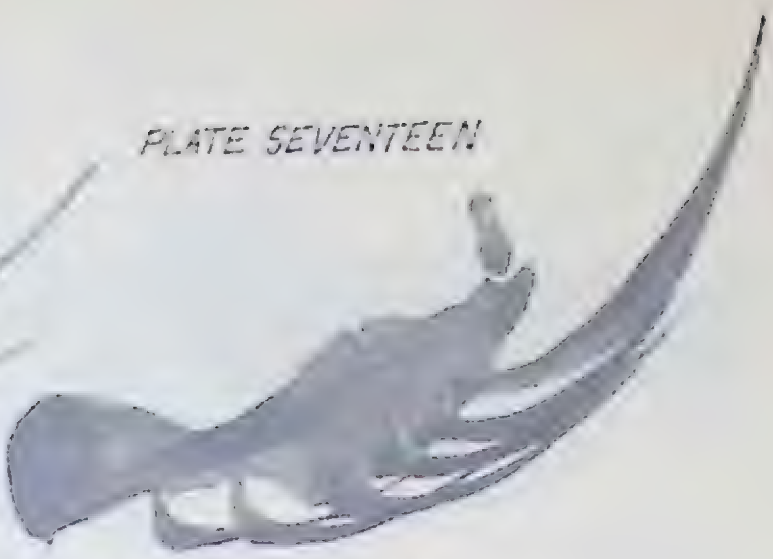
Parupeneus multifasciatus
Mullidae
PERCIFORMES

Branchiostegal series and hyoid arch in Acanthopterygii.

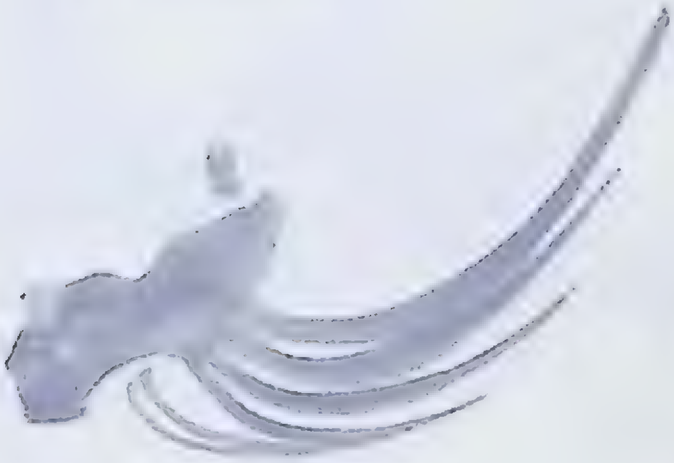
PLATE SEVENTEEN



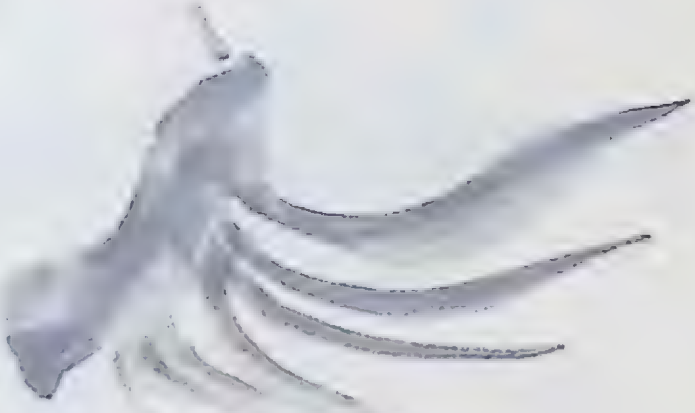
Eucinostomus sp
Leiognathidae
PERCIFORMES



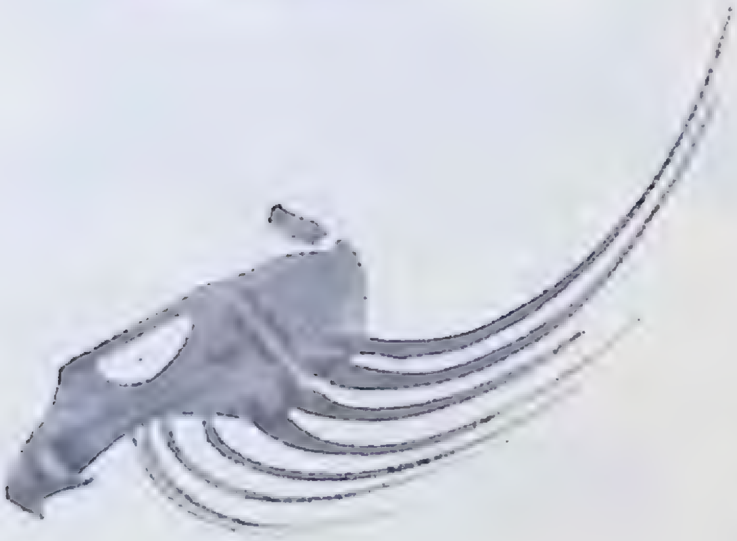
Priacanthus cruentatus
Priacanthidae
PERCIFORMES



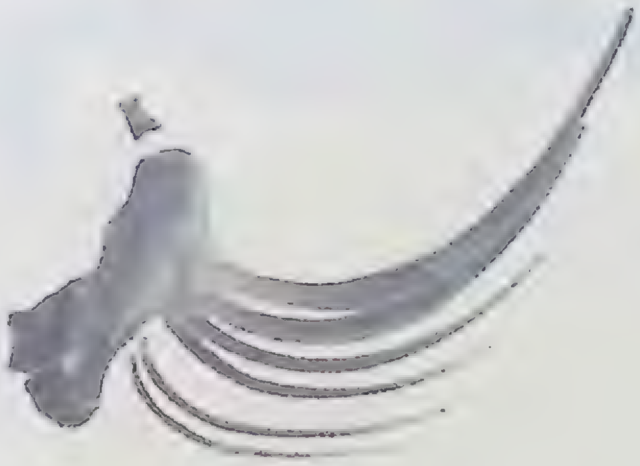
Stenotomus caprinus
Sparidae
PERCIFORMES



Menticirrhus littoralis
Sciaenidae
PERCIFORMES



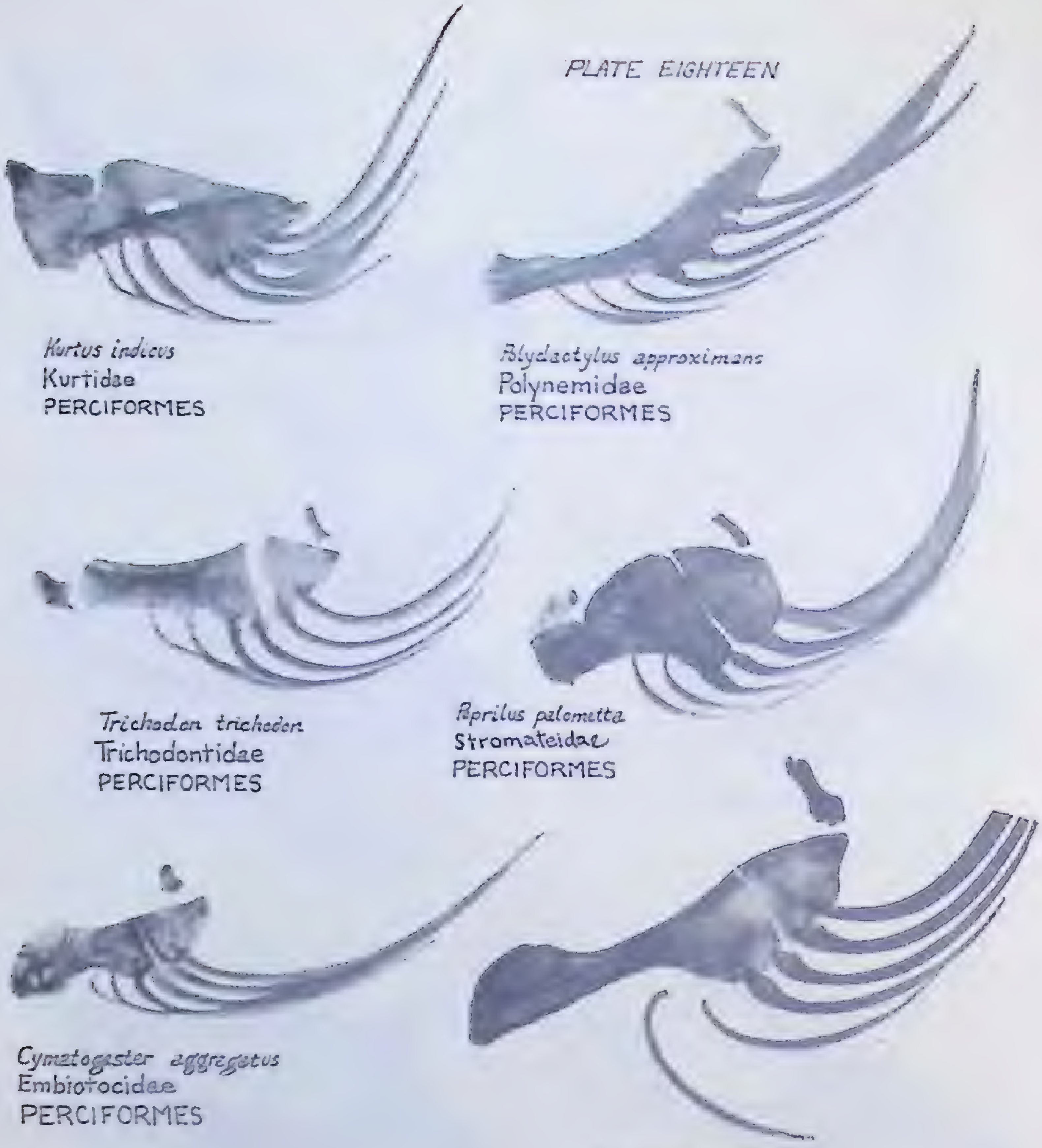
Trachinotus falcatus
Carangidae
PERCIFORMES



Kyphosus sectatrix
Kyphosidae
PERCIFORMES

Branchiostegal series and hyoid arch in Acanthopterygii.

PLATE EIGHTEEN



Kurtus indicus
Kurtidae
PERCIFORMES

Polydactylus approximans
Polynemidae
PERCIFORMES

Trichodon trichodon
Trichodontidae
PERCIFORMES

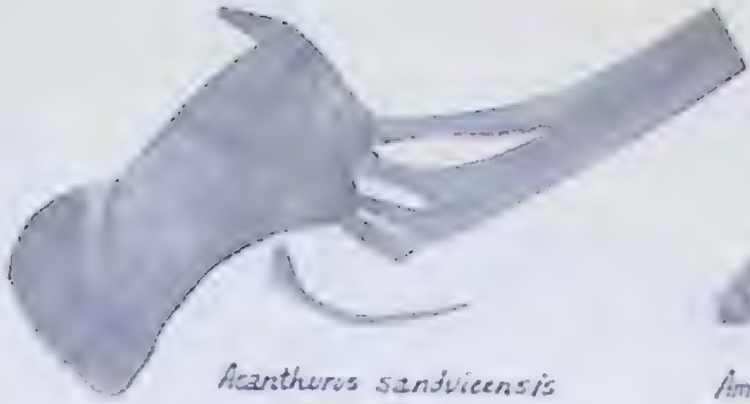
Peprilus palometta
Stromateidae
PERCIFORMES

Cymatogaster aggregatus
Embiotocidae
PERCIFORMES

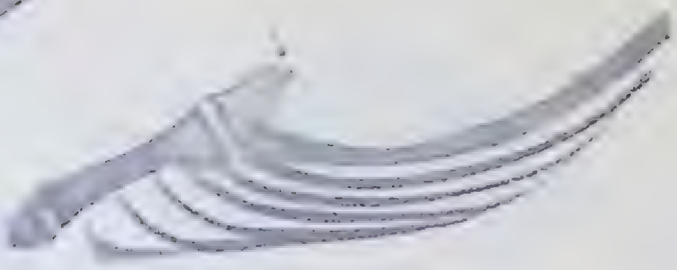
Trematomus bernachii
Nototheniidae
PERCIFORMES

Branchiostegal series and hyoid arch in Acanthopterygii.

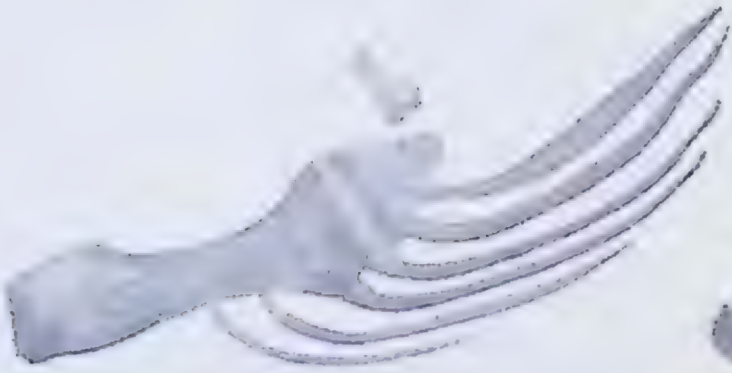
PLATE NINETEEN



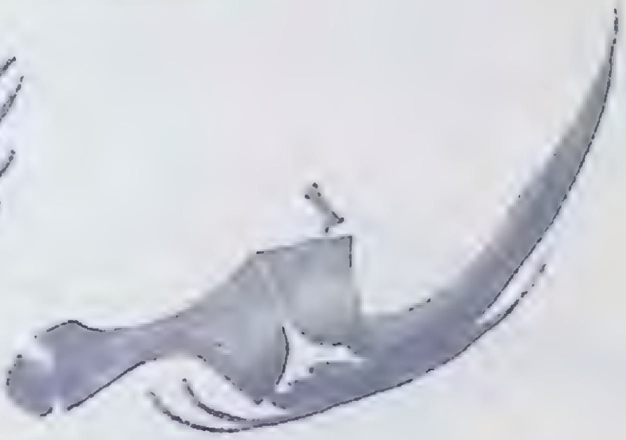
Acanthurus sandvicensis
Acanthuridae
PERCIFORMES



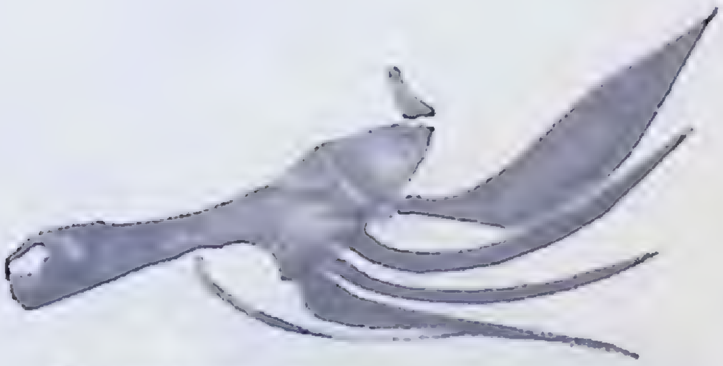
Ammodytes hexapterus
Ammodytidae
PERCIFORMES



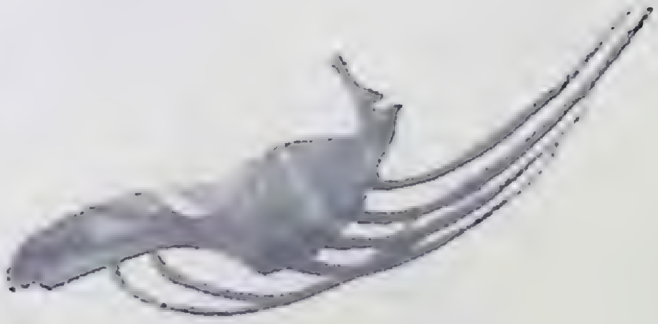
Macrozoarces anguillaris
Zoarcidae
PERCIFORMES



Gobiomorus maculatus
Eleotridae
PERCIFORMES



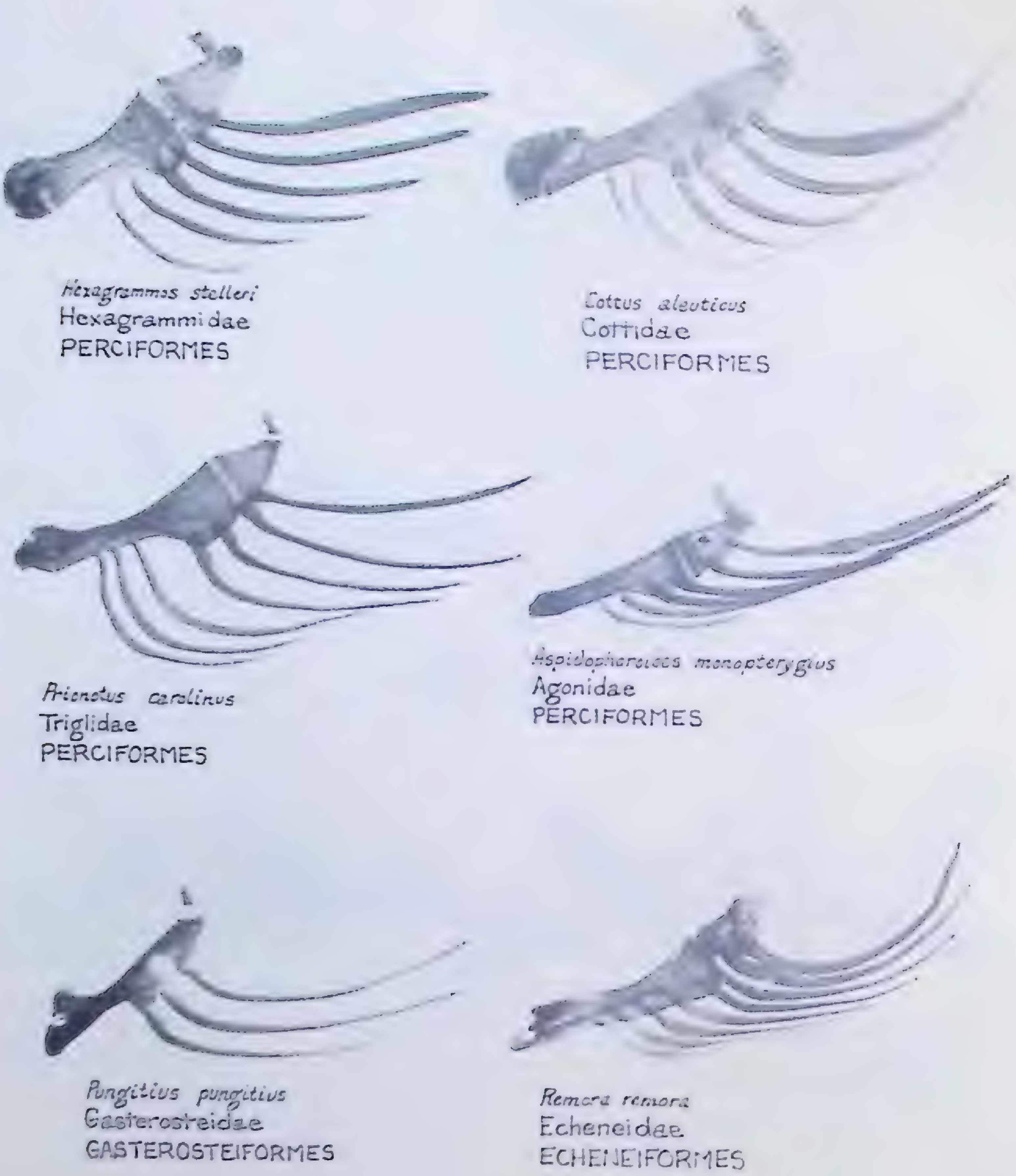
Bathygobius ramosus
Gobiidae
PERCIFORMES



Liparis atlanticus
Liparidae
PERCIFORMES

Branchiostegal series and hyoid arch in Acanthopterygii.

PLATE TWENTY



Hexagrammos stelleri
Hexagrammidae
PERCIFORMES

Cottus aleuticus
Cottidae
PERCIFORMES

Prionotus carolinus
Triglidae
PERCIFORMES

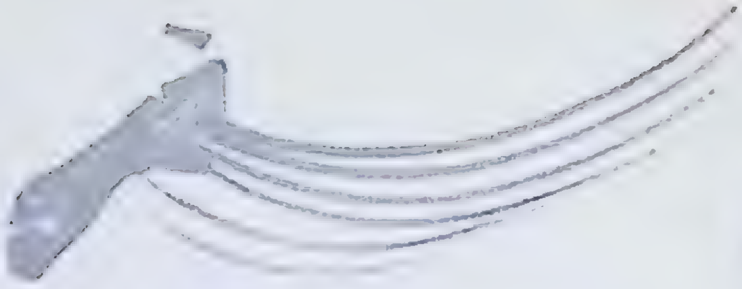
Aspidophoroides monopterygius
Agonidae
PERCIFORMES

Pungitius pungitius
Gasterosteidae
GASTEROSTEIFORMES

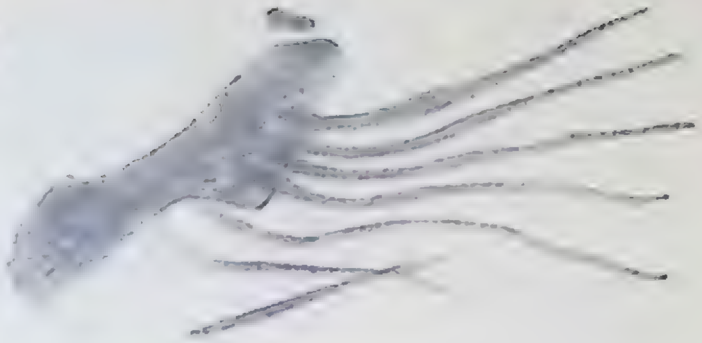
Remora remora
Echeneidae
ECHENEIFORMES

Branchiostegal series and hyoid arch in Acanthopterygii.

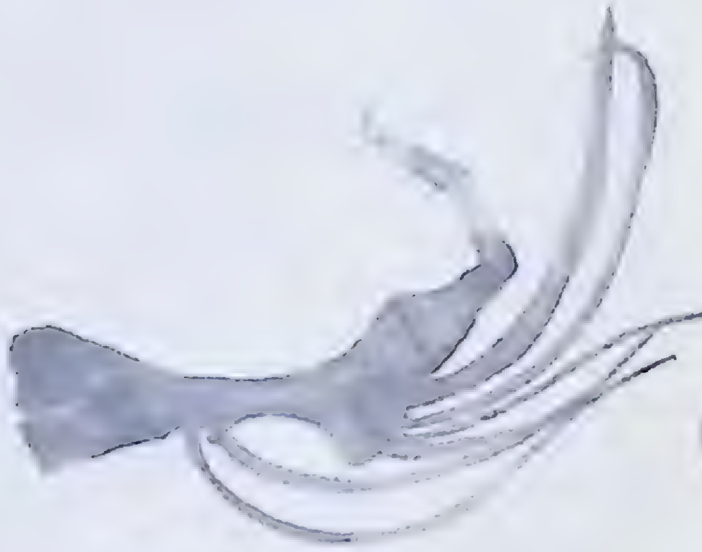
PLATE TWENTY-ONE



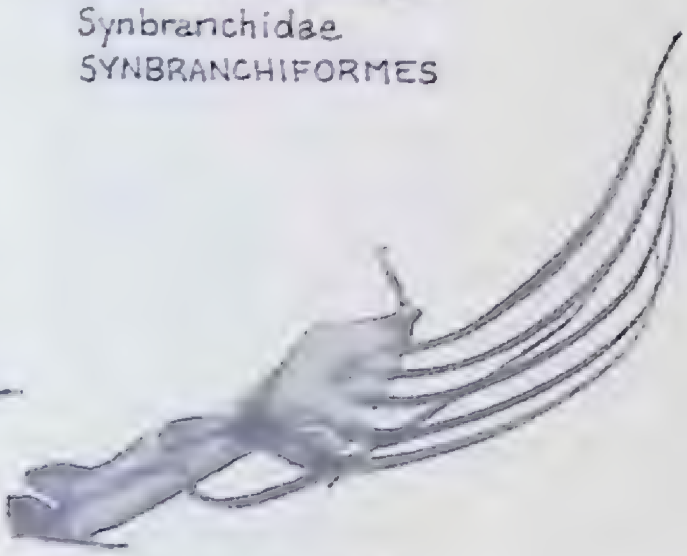
Mastacembelus armatus
Mastacembelidae
MASTACEMBELIFORMES



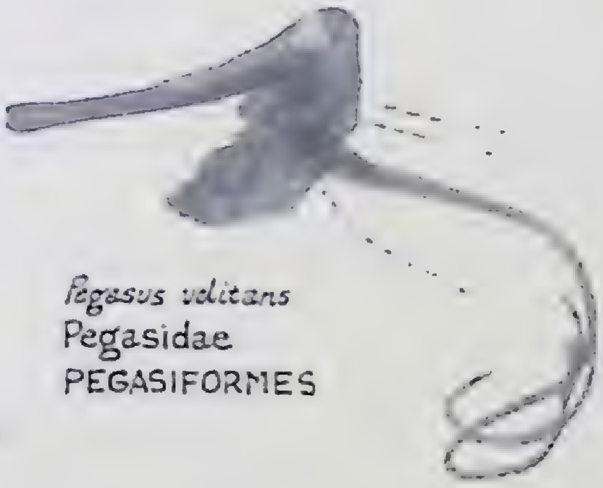
Synbranchus marmoratus
Synbranchidae
SYNBRANCHIFORMES



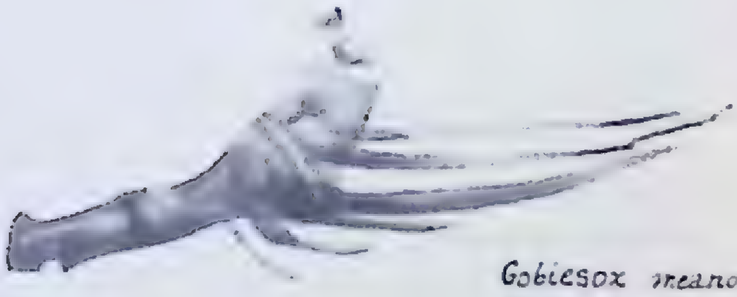
Antennarius drombus
Antennariidae
LOPHIIFORMES



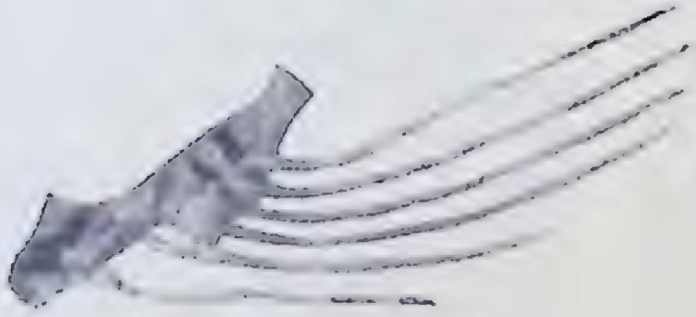
Porichthys notatus
Batrachoididae
BATRACHOIDIFORMES



Pegasus volitans
Pegasidae
PEGASIFORMES



Gobiesox meandricus
Gobiesocidae
GOBIESOCIFORMES



Chaudhuria caudata
Chaudhuriidae
MASTACEMBELIFORMES

Branchiostegal series and hyoid arch in Acanthopterygii.

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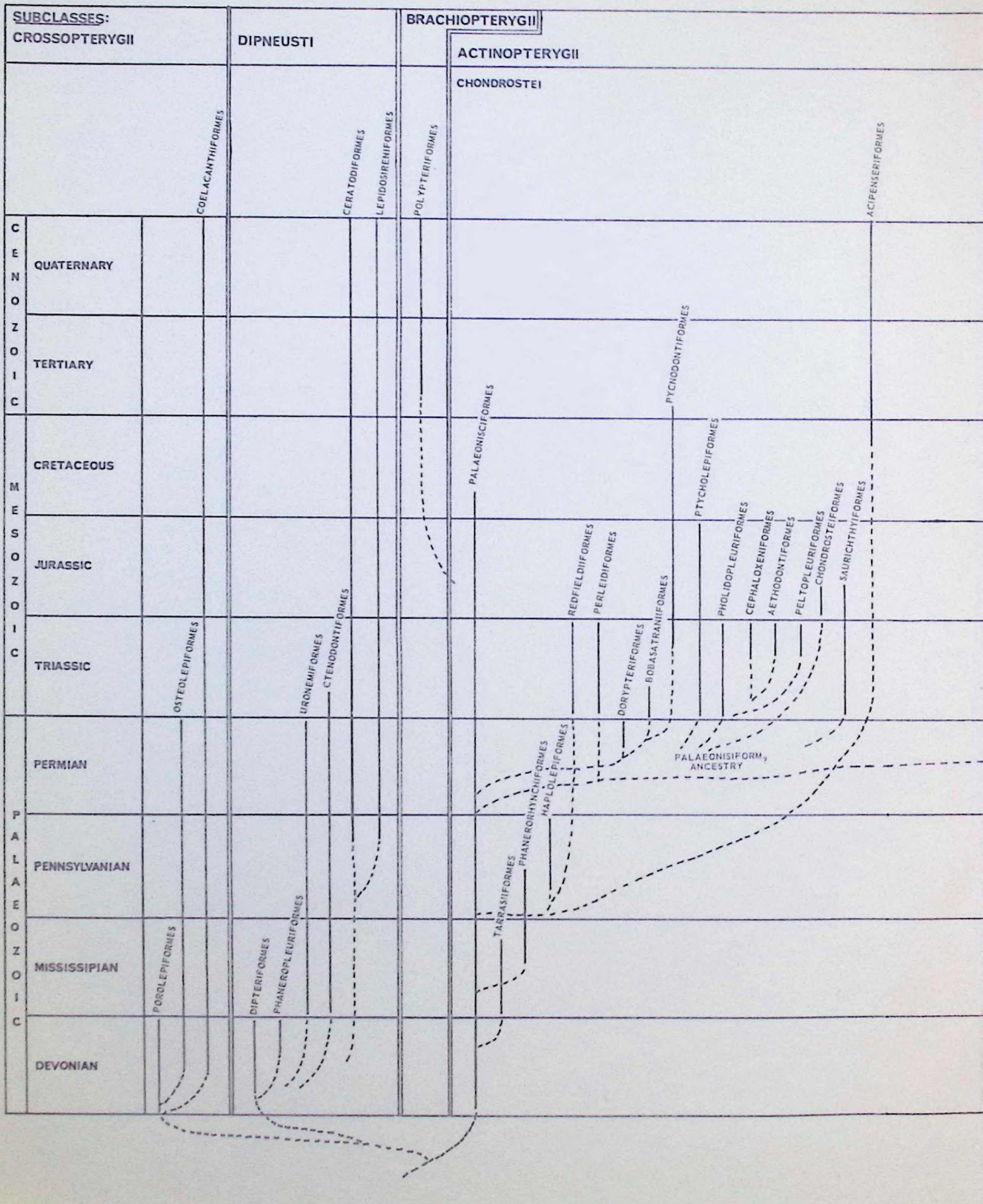
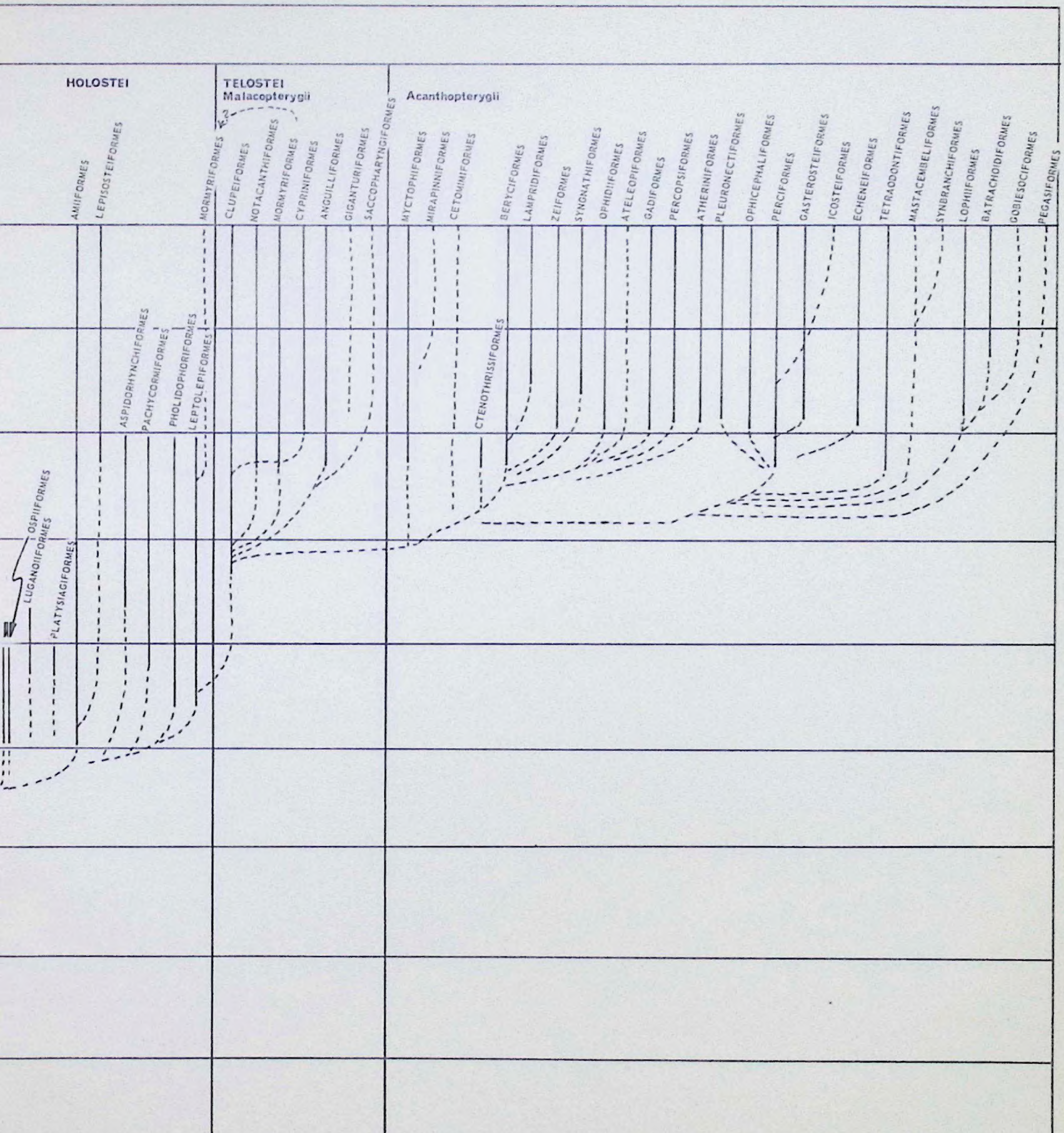

SUBCLASSES:
CROSSOPTERYGII
DIPNEUSTI
BRACHIOPTERYGII
ACTINOPTERYGII
CHONDROSTEI
COELACANTHIFORMES
CERATODIFORMES
LEPIDOSIRENIFORMES
POLYPTERIFORMES
ACIPENSERIFORMES
CENOZOIC
QUATERNARY
TERTIARY
MESOZOIC
CRETACEOUS
JURASSIC
TRIASSIC
PALAEOZOIC
PERMIAN
PENNSYLVANIAN
MISSISSIPIAN
DEVONIAN
PYCNODONTIFORMES
PALAEONISCIFORMES
PTYCHOLEPIFORMES
REDFIELDIIFORMES
PERLEIDIFORMES
BOBASATRANIIFORMES
DORYPTERIFORMES
PHOLIDOPLEURIFORMES
CEPHALOXENIFORMES
AETHODONTIFORMES
PELTOPLEURIFORMES
CHONDROSTEIFORMES
SAURICHTHYIFORMES
OSTEOLEPIFORMES
URONEMIFORMES
CTENODONTIFORMES
PALAEONISIFORM,
ANCESTRY
HAPLOLEPIFORMES
PHANERORHYNCHIFORMES
TARRASIIFORMES
PHANEROPLEURIFORMES
DIPTERIFORMES
POROLEPIFORMES


HOLOSTEI
TELOSTEI
Malacopterygii
Acanthopterygii
?
AMIIFORMES
LEPISOSTEIFORMES
ASPIDORHYNCHIFORMES
PACHYCORMIFORMES
PHOLIDOPHORIFORMES
LEPTOLEPIFORMES
OSPIIFORMES
LUGANOIIFORMES
PLATYSIAGIFORMES
MORMYRIFORMES
CLUPEIFORMES
NOTACANTHIFORMES
MORMYRIFORMES
CYPRINIFORMES
ANGUILLIFORMES
GIGANTURIFORMES
SACCOPHARYNGIFORMES
MYCTOPHIFORMES
MIRAPINNIFORMES
CETOMIMIFORMES
CTENOTHRISSIFORMES
BERYCIFORMES
LAMPRIDIFORMES
ZEIFORMES
SYNGNATHIFORMES
OPHIDIIFORMES
ATELEOPIFORMES
GADIFORMES
PERCOPSIFORMES
ATHERINIFORMES
PLEURONECTIFORMES
OPHICEPHALIFORMES
PERCIFORMES
GASTEROSTEIFORMES
ICOSTEIFORMES
ECHENEIFORMES
TETRAODONTIFORMES
MASTACEMBELIFORMES
SYNBRANCHIFORMES
LOPHIIFORMES
BATRACHOIDIFORMES
GOBIESOCIFORMES
PEGASIFORMES